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ON

THE ARCHETYPE AND HOMOLOGIES

OF

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THE VERTEBRATE SKELETON.

BY

RICHARD OWEN, F.R.S.

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TO

WILLIAM JOHN BRODERIP, ESQ.,

F.R.S., F.G.S., F.L.S., &c.

My dear Broderip,

The interest which you have taken in the progress of the researches that are embodied in the present Treatise on the Vertebrate Archetype induces me to dedicate it to you: and I am happy in having this opportunity of gratefully acknowledging your excellent guidance by which my early studies in Zoology were facilitated, and of expressing the affection and esteem with which I am,

Your sincere Friend,

RICHARD OWEN.

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The subject of the following Essay has occupied a portion of my attention from the period when, after having made a certain progress in Comparative Anatomy, the evidences of a greater conformity to type, especially in the bones of the head of the Vertebrate animals, than the immortal Cuvier had been willing to admit, began to enforce a reconsideration of his conclusions, to which I had previously yielded implicit assent. The results*, in so far as they seemed to be fairly sustained by observation of facts, have been successively communicated to the Royal College of Surgeons of England in my Hunterian Lectures for 1844 and subsequent years; and in 1846 I availed myself of the peculiar advantages afforded by the 'British Association for the Advancement of Science' to bring my general views on the Archetype and Homologies of the Vertebrate Skeleton before the British and Foreign Anatomists assembled at the meeting of the Association at Southampton, in order to submit them to the test of a discussion which could not have been so fully carried out under any other circumstances in this country, where Homological Anatomy had previously excited little

---

* Those illustrated by the skeleton of fishes are given in the 'Lectures on the Comparative Anatomy and Physiology of the Vertebrate Animals,' Part 1. 1846.

attention, and had remained almost in the state in which it was left by Cuvier and Geoffroy St. Hilaire.

The interest which has since been expressed on the subject of those communications, published as a 'Report' in the Transactions of the British Association for 1846, and the wish to make the matter of that 'Report' more accessible and intelligible to students of anatomy, have induced me to reprint it in a separate form, with some additional facts and illustrations.

I beg to express my obligations to the President and Council of the British Association for the permission to reprint the substance of my Report, and for the liberal use of the woodcuts with which it was illustrated. And I am glad here to have the opportunity to acknowledge the valuable aid which I derived from the skill and care and patience of Mr. Frederick Gyde, the wood-engraver, in rendering accurately the numerous details and references in the figures, and to express similar acknowledgements to Mr. Tuffen West, the lithographer of the plates.

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ON

THE ARCHETYPE AND HOMOLOGIES

OF

THE VERTEBRATE SKELETON.

Chapter I.—Special Homology.

Introduction.

WHEN the structure of organized beings began to be investigated, the parts, as they were observed, were described under names or phrases suggested by their forms, proportions, relative position, or likeness to some familiar object. Much of the nomenclature of human anatomy has thus arisen, especially that of the osseous system, which, with the rest of man's frame, was studied originally from an insulated point of view, and irrespective of any other animal structure or any common type.

So when the exigences of the veterinary surgeon, or the desire of the naturalist to penetrate beneath the superficial characters of his favourite class, led them to anatomise the lower animals, they, in like manner, seldom glanced beyond their immediate subject, and often gave arbitrary names to the parts which they detected. Thus the dissector of the horse, whose attention was more especially called to the leg as the most common seat of disease in that animal, specified its 'cannon-bone,' its 'great' and 'small' pastern-bones, its 'coffin-bone,' and its 'nut-bone' or 'coronet': some cranial bones were also named agreeably with their shape, as the 'os quadratum,' for example. The ornithotomist described, in the same irrelative manner, the 'ossa homoidea,' 'ossa communicantia' or 'interarticularia,' the 'columella' and 'os furcatorium.' Petit* had his 'os grele' and 'os en massue;' Herissant† his 'os carré'; which, however, is by no means the same bone with the 'os carré' or 'os quadratum' of the hippotomist. The investigator of reptilian osteology described 'hatchet-bones' and chevron-bones, an 'os annulare' or 'os en ceinture,' and an 'os transversum': he likewise defined a 'columella'; but this was a bone quite distinct from that so called in the bird. The ichthyotomist had also an 'os transversum,' which again was distinct from that in reptiles, and he demonstrated his 'os discoideum,' 'os cœnosteon,' 'os mystaceum,' 'ossa symplectica prima,' 'secunda,' 'tertia,' 'suprema,' 'postrema,' &c. Similar examples of arbitrary names might easily be multiplied; many distinct ones signifying the same part in different animals, whilst essentially distinct parts often received the same name from different anatomical authors, occupied exclusively by particular species. Each, at the beginning, viewed his subject independently; and finding, therefore, new organs, created a new nomenclature for them; just as the anthropotomist had done, of necessity, when, with a view to the cure or relief of disease and injury, he entered upon the vast domain of anatomical science by the structure of Man, or of the mammals most resembling Man.

---

* Observations Anatomiques sur les mouvemens du bec des Oiseaux, Mémoires de l'Acad. des Sciences, 1748, p. 345.

† Mém. de l'Acad. des Sciences, 1774, p. 497.

It may well be conceived with what a formidable load of names the memory must have been burthened, if any could have been found equal to it, had the anatomy of animals continued and made progress under its primitive condition of an assemblage of arbitrarily described and uncompared facts.

Happily the natural tendency of the human mind to sort and generalize its ideas could not long permit such a state of the science, if science it could be called, to remain. A large and valuable portion of the labours of the comparative anatomists who have honoured the present century, has been devoted to the determination of those bones in the lower animals which correspond with bones in the human skeleton; the results being usually expressed by applying to the parts so determined the same names, as far as the nomenclature of anthropotomy allowed. Few, however, of the parts of the human body have received single substantive names; they are for the most part indicated by shorter or longer descriptive phrases, like the species and parts of plants before Linnæus reformed botanical nomenclature.

The temptation to devise a systematic Nomenclature of Anatomy, generally applicable to all animals, increases with the advance of the science, and from the analogy of what has taken place in other sciences it may one day be yielded to and exercise the ingenuity of some ardent reformer. But the same analogy, especially that afforded by chemical science since the time of Lavoisier, would rather lead the true friend of anatomy to deprecate the attempt to impose an entirely new nomenclature of parts, however closely expressive of the nature and results of the science at the period when it might be devised. For there is no stability in such descriptive or ennunciative nomenclature; it changes, and must change with the progress of the science, and thus becomes a heavy tax upon such progress.

If the arbitrary term 'calomel,' which, like 'house' and 'dog,' signifies the thing in its totality, without forcing any particular quality of its subject prominently upon the mind, be preferable, on that account as well as its brevity, to the descriptive phrases 'submuriate of mercury,' 'chloride of mercury,' or 'proto-chloride of mercury,' in enunciating propositions respecting the substance to which it is applied; and if it possesses the additional advantage of fixity, of a steady meaning not liable to be affected, like a descriptive name or phrase, by every additional knowledge of the properties of the substance; the anatomist, zealous for the best interests of his science, will feel strongly the desirableness of retaining and securing for the subjects of his propositions similar single, arbitrary terms, especially if they are also capable of being inflected and used as noun adjectives.

The practice of anatomists of the soundest judgement has usually been, to transfer the anthropotomical term or phrase to the answerable part when detected in other animals. The objection that the original descriptive or otherwise allusive meaning of the term seldom applies to the part with equal force in other animals, and sometimes not at all, is one of really little moment; for the term borrowed from anthropotomy is soon understood in an arbitrary sense, and without regard to its applicability to the modified form which the namesake of the human bone commonly assumes to suit the ends required in the lower species. No anatomist, for example, troubles himself with the question of the amount of resemblance to a crow's or other bird's beak in the 'coracoid' bone of a reptile, or with the want of likeness of the kangaroo's 'coccyx' to the beak of a cuckoo; or of the whale's 'vomer' to a ploughshare; or ever associates the idea of the original mystic allusion in the anatomical term 'sacrum' with his description of that bone in the megatherium or other monster. Common sense gratefully accepts such names when they become as arbitrary as cat or calomel, and when such concretes or adjectives as 'coccygeal,' 'vomerine' and 'sacral' can be employed to teach the properties or accidents of their subjects.

To substitute names for phrases is not only allowable, but I believe it to be indispensable to the right progress of anatomy; but such names must be arbitrary, or, at least, should have no other signification than the homological one, if anatomy, as the science of the structure of all animals, is to enjoy the inestimable benefit of a steady and universal nomenclature. I am far from being insensible to the advantages which other sciences have derived from revolutions in their technical language; but experience has also demonstrated attendant evils; and these, it is to be feared, would preponderate in the case of anatomy, on account of the peculiar character of its origin, and the fact of its cultivators being for the most part introduced to the science through the portal of anthropotomy. So long, likewise, as due deference continues to be paid to the deep and vital importance of the practical applications of the parent science in medicine and surgery, it will be in vain for any man to expect that his sole authority would suffice for the general reception of an entirely new nomenclature, however philosophically devised or clearly enunciative of the highest and most comprehensive truths of the science at the time of its formation.

After maturely considering this subject in its various relations, I have arrived at the conviction that the best interests of anatomical science will be consulted by basing the nomenclature applicable to the vertebrate subkingdom upon the terms and phrases in which the great anthropotomists of the 16th, 17th and 18th centuries have communicated to us the fruits of their immortal labours. For it is only on this firm foundation that we may hope to avoid that ceaseless change of terms which follows the device of a systematic nomenclature significant of a given progress and result of scientific research. But the names of the parts of the vertebrate animals so based on or deduced from the language of anthropotomy must divest themselves of their original descriptive signification, and must stand simply and arbitrarily as the signs of such parts, or at least with the sole additional meaning of indicating the relation of the part in the lower animal to its namesake or homologue in Man. It is an old maxim accepted by the best logicians, that no name is so good as that which signifies the total idea or whole subject, without calling prominently to mind any one particular quality, which is thereby apt to be deemed, undeservedly, more essential than the rest.

The chief improvement which the language of anatomy, based upon that of anthropotomy, must receive in order to do its requisite duty, is the substitution of 'names' for 'phrases' and 'definitions'; and this is less a change of nomenclature than the giving to anatomy what it did not before possess, but which is absolutely requisite to express briefly and clearly, and without periphrasis, propositions respecting the parts of animal bodies. Such names should be derived from a universal or dead language, and when anglicized, or translated into other modern equivalents, ought to be capable of being inflected adjectively.

A few examples will suffice to show how greatly the advantage of such names preponderates over the trouble of substituting them in the memory for the definitions which previously signified the ideas.

In the classical Anthropotomy of Soemmerring, a well-defined part of the skull, which is a distinct bone in the human embryo, and permanently so in all cold-blooded Vertebrata, is called "pars occipitalis stricte sic dicta partis occipitalis ossis spheno-occipitalis[*]." Monro, in his justly-esteemed treatise 'On the Human Bones[†],' defines the same bone as "all the part of the (occipital) bone above the great foramen." In the 'Elements of Anatomy,' by Dr. Quain[‡], a work of repute for its clearness and minuteness of detail, the part in question is neither named nor described. The term *supra-occipitale*, Lat. (*supra-occipital*, Eng., *sur-occipital*, Fr.), is obviously a gain to anatomical science in all propositions respecting this part in the vertebrate series.

Certain parts of a vertebra, distinct bones at an early period in man, and throughout life in most reptiles, are defined by Soemmerring as 'radices arcûs posterioris vertebræ,' or 'arcus posterior vertebræ' collectively[§]. Monro describes the same parts separately, as "a broad oblique bony plate extended backwards," and together, as "a bony arch produced backwards": he names, defines and minutely describes the processes, &c. of these bony plates, which in the series of Vertebrata are soon found to be non-essential characters; but for the plates themselves, which are the most constant and essential constituents of a vertebra, he has no name. Dr. Quain defines the same parts as "two plates of bone, the lamellæ or arches, which complete the central foramen[‖]." They are sometimes more briefly but vaguely spoken of in English works of Comparative Anatomy as "the vertebral lamellæ" or "vertebral laminæ," or "perivertebral elements." The term '*neurapophysis*,' Lat. and Eng. ('*neurapophyse*,' Fr.), applicable to each element individually, under which all its properties may be predicated of by the adjective 'neurapophysial,' without periphrasis, seems by its adoption in the classical works of MM. Agassiz and Stannius, to be as acceptable as the term 'sur-occipital' substituted by Cuvier for the definitions in anthropotomy above cited.

Similar instances of the absence of determinate names, capable of inflection, for parts of the human frame, will be seen in the last column of Table I., and others will occur to the anatomist, even in regard to most important parts, as the primary natural divisions of the neural axis, for example, to the great hindrance of brief, clear and intelligible descriptions. So long as the phrases 'marrow of the spine,' 'chord of the spine,' continue to usurp the place of a proper name, all propositions concerning their subject must continue to be periphrastic, and often also dubious. Thus if the pathologist, speaking of diseases of the spinal marrow, desires to abbreviate his proposition by speaking of 'spinal disease,' he is liable to be misunderstood as referring to disease of the spinal or vertebral column. The vague, but often-used phrase 'chorda dorsalis' for the embryonic fibro-gelatinous basis of the spine, adds another source of confusion likely to arise from the use of the term 'spinal chord,' as applied to that most important part of the neural axis which I have proposed to call 'Myelon[¶],' a term which, if adopted, would be attended by this advantage, that no ambiguity could arise in speaking of 'myelonal functions,' 'myelonal affections,' or other properties of this part of the central axis of the nervous system.

Anthropotomy, in respect to its nomenclature, or rather the want of one, is, as I have already remarked, not unlike what botany was before the time of Linnæus, and we may anticipate the happiest effects from a judiciously reformed technical language in the advancement of the true and philosophic knowledge of the human structure, from the rapid progress of botany when the opposition raised by sloth or envy to the Linnæan reforms was overcome. For a good general anatomical nomenclature, based and regulated upon the principles above defined, must reflect its benefits upon anthropotomy. I dare not flatter myself that the names adopted or proposed for the Osseous System of the Vertebrata in my 'Hunterian Lectures' and in the first column of Table I. will meet at once with acceptance, but the attempt to establish such a nomenclature will be felt to have been an indispensable step in undertaking a general survey of the homological relations of the vertebrate skeleton.

---

[*] De Corporis Humani Fabrica, 1794, t. i. p. 162.

[†] Kirby's edition, 8vo, 1820, p. 76.

[‡] Elements of Descriptive and Practical Anatomy, 8vo, 1828, p. 50.

[§] De Corporis Humani Fabrica, 1794, t. i. pp. 235, 236.

[‖] Elements of Descriptive and Practical Anatomy, 8vo, 1828, p. 121.

[¶] Hunterian Lectures, vol. ii. 'Vertebrata,' part i. p. 172.

In proposing a definite name for each distinct bone, declaratory of its special homology throughout the vertebrate kingdom, I have sought earnestly to reduce the amount of reform to the minimum allowed by the exigences of the case. Agreeably with Aphorism III. of the 'Philosophy of the Inductive Sciences' (p. lxvii.), the nomenclature of anthropotomy forms the basis, and all the names given to parts by one or other of the great French anatomists have been accepted, with the modifications of a Latin or an English termination, wherever such names had not been applied, as is the case with some proposed by Geoffroy St. Hilaire, to two different parts. In substituting names for phrases, I have endeavoured, conformably with another of Dr. Whewell's canons (Aph. XVII. *op. cit.* p. cxvii.), to approximate the sound of the name as nearly as possible to those of the leading terms of the definition or phrase, as e. g. *alisphenoid* for 'ala media, &c. sphenoidalis' and for 'grande aile du sphénoïde'; *orbitosphenoid* for 'ala superior seu orbitalis, &c. sphenoidalis,' and for 'aile orbitaire du sphénoïde*.'

The corresponding parts in different animals being thus made namesakes, are called technically 'homologues.' The term is used by logicians as synonymous with 'homonyms,' and by geometricians as signifying 'the sides of similar figures which are opposite to equal and corresponding angles,' or to parts having the same proportions†: it appears to have been first applied in anatomy by the philosophical cultivators of that science in Germany. Geoffroy St. Hilaire says, "Les organes des sens sont *homologues*, comme s'exprimerait la philosophie Allemande; c'est-à-dire qu'ils sont analogues dans leur mode de développement, s'il existe véritablement en eux un même principe de formation, une tendance uniforme à se répéter, à se reproduire de la même façon‡." The French anatomist, however, seems not rightly to define the sense in which the German philosophers have used the term: there is a looseness in the expression 'analogous in their mode of development,' which may mean either identical or similar, and also different kinds of similarity. Parts are homologous in the sense in which the term is used in this Work, which are not always similarly developed: thus the 'pars occipitalis stricte sic dicta,' &c. of Soemmerring is the special homologue of the supraoccipital bone of the cod, although it is developed out of pre-existing cartilage in the fish and out of aponeurotic membrane in the human subject. I also regard the supraoccipital as the serial homologue of the parietal and the midfrontal, although these are developed out of the epicranial membrane in the fish, and not out of pre-existing cartilage, like the supraoccipital. The femur of the cow is not the less homologous with the femur of the crocodile, because in the one it is developed from four separate ossific centres, and the other from only one such centre. In like manner the compound mandibular ramus of the fish is the homologue of the simple mandibular ramus of the mammal, as the compound tympanic pedicle of the fish is homologous with the simple tympanic pedicle of the bird, the differences expressed by the terms 'simple' and 'compound' depending entirely on a difference of development.

---

* The happy facility of combination which the German language enjoys has long enabled the very eminent anatomists of that intellectual part of Europe to condense the definitions of anthropotomy into single words; but these cannot become cosmopolitan; such terms as 'Hinterhauptbeinkörper,' 'Schläfbeinschüppen,' and 'Zwischenkiemendeckelstück,' are likely to be restricted to the anatomists of the country where the vocal powers have been trained from infancy to their utterance.

† This is the sense in which the term is defined in the French Dictionary and in our Johnson's Dictionary.

‡ Annales des Sciences Naturelles, tom. vi. 1825, p. 341.

Without knowing the precise sense in which Geoffroy St. Hilaire understood 'analogous development,' one cannot determine how much or how little it is applicable to the determination of homologies or to the definition of homologous parts. Dr. Reichert seems to have been unduly influenced by the idea of 'analogy or similarity of development in the determination of homologous parts' when he rejected the parietal and frontal bones from the system of the endo-skeleton, because they were not developed from a pre-existing cartilaginous basis*, or, because they could be easily detached from subjacent persistent cartilage in certain fishes; the essential distinction between these and the supra-occipital in regard to development being, that whereas the cartilaginous stage intervened in the latter between the membranous and the osseous stages, in the other, usually more expanded, cranial spines, the osseous change appears to be immediately superinduced upon the primitive aponeurotic histological condition.

M. Agassiz seems, in like manner, to give undue importance to similarity of development in the determination of homologies, where he repudiates the general homology of the basi-sphenoid with the vertebral centrum, and consequently its serial homology with the basi-occipital, because the pointed end of the chorda dorsalis has not been traced further forwards along the basis of the cranium in the embryo osseous fish than the basi-occipital†. But the development of the centrum of every vertebra begins, not in the gelatinous chord, but in its aponeurotic capsule, and it is in the expanded aponeurosis directly continued from the 'chorda' along the 'basis cranii' that the thin stratum of cartilage-cells is formed from which the ossification of the basi-sphenoid, presphenoid and vomer proceeds.

There exists doubtless a close general resemblance in the mode of development of homologous parts; but this is subject to modification, like the forms, proportions, functions and very substance of such parts, without their essential homological relationships being thereby obliterated. These relationships are mainly, if not wholly, determined by the relative position and connection of the parts, and may exist independently of form, proportion, substance, function and similarity of development. But the connections must be sought for at every period of development, and the changes of relative position, if any, during growth, must be compared with the connections which the part presents in the classes where vegetative repetition is greatest and adaptive modification least.

Relations of homology are often not only confounded with those of analogy, but in some recent and highly estimable works on comparative anatomy the terms 'analogy' and 'analogue' continue to be used to express the ideas of homology and homologue, or are so used as to leave in doubt the meaning of the author. Thus when we read in the latest edition of the 'Leçons d'Anatomie Comparée' of Cuvier, "Les branchies sont les poumons des animaux absolument aquatiques," t. vii. p. 164; and with regard to the cartilaginous or osseous supports of the gills, "elles sont, à notre avis, aux branchies des poissons, ce que les cerceaux cartilagineux ou osseux des voies aériennes sont aux poumons des trois classes supérieures," *Ibid.* p. 177, we are left in doubt whether it is meant that the gills and their mechanical supports merely perform the same function in fishes which the lungs and windpipe do in mammals, or whether they are not also actually the same parts differently modified in relation to the different respiratory media in the two classes of animals. The deeper-thinking Geoffroy leaves no doubt as to his meaning where he argues in the 'Philosophie Anatomique' (8vo, 1818, 4ième mémoire, p. 205), that the branchial arches of fishes are the modified tracheal rings of the air-breathing vertebrates: we perceive at once that he is enunciating a relation of homology.

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* Vergleichende Entwickelungsgeschichte des Kopfes der nackten Reptilien, 4to, 1838, pp. 212, 218.

† Recherches sur les Poissons Fossiles, 4to, 1843, i. p. 127.

I have elsewhere[*] discussed the relations, both homological and analogical, of the respiratory organs of the air-breathing and water-breathing vertebrate animals, and have here adverted to them merely to illustrate the essential distinction of those relations. In the 'Glossary' appended to the first volume of my 'Hunterian Lectures,' the terms in question are defined as follows:—

"ANALOGUE."—A part or organ in one animal which has the same function as another part or organ in a different animal.

"HOMOLOGUE."—The same organ in different animals under every variety of form and function[†]."

The little 'Draco volans' offers a good illustration of both relations. Its fore-limbs being composed of essentially the same parts as the wings of a bird are homologous with them; but the parachute being composed of different parts, yet performing the same function as the wings of a bird, is analogous to them. Homologous parts are always, indeed, analogous parts in one sense, inasmuch as, being repetitious of the same parts of the body, they bear in that respect the same relation to different animals. But homologous parts may be, and often are, also analogous parts in a fuller sense, viz. as performing the same functions: thus the fin or pectoral limb of a Porpoise is homologous with that of a Fish, inasmuch as it is composed of the same or answerable parts: and they are the analogues of each other, inasmuch as they have the same relation of subserviency to swimming. So, likewise, the pectoral fin of the flying-fish is analogous to the wing of the Bird, but, unlike the wing of the Dragon, it is also homologous with it.

Relations of homology are of three kinds: the first is that above defined, viz. the correspondency of a part or organ, determined by its relative position and connections, with a part or organ in a different animal; the determination of which homology indicates that such animals are constructed on a common type: when, for example, the correspondence of the basilar process of the human occipital bone with the distinct bone called 'basi-occipital' in a fish or crocodile is shown, the *special homology* of that process is determined.

A higher relation of homology is that in which a part or series of parts stands to the fundamental or general type, and its enunciation involves and implies a knowledge of the type on which a natural group of animals, the vertebrate for example, is constructed. Thus when the basilar process of the human occipital bone is determined to be the 'centrum' or 'body of the last cranial vertebra,' its *general homology* is enunciated.

If it be admitted that the general type of the vertebrate endo-skeleton is rightly represented by the idea of a series of essentially similar segments succeeding each other longitudinally from one end of the body to the other, such segments being for the most part composed of pieces similar in number and arrangement, and though sometimes extremely modified for special functions, yet never so as to wholly mask their typical character,—then any given part of one segment may be repeated in the rest of the series, just as one bone may be reproduced in the skeletons of different species, and this

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[*] Lectures on Vertebrata, 1846, p. 279.

[†] Lectures on Invertebrate Animals, 8vo, 1843. Glossary, pp. 374, 379. My ingenious and learned friend Mr. Hugh Strickland has made a strong and able appeal to the good sense of comparative anatomists in favour of the restriction of these terms to the senses in which they are here defined.—Phil. Mag. 1846, pp. 358, 362.

kind of repetition or representative relation in the segments of the same skeleton I call 'serial homology.' As, however, the parts can be namesakes only in a general sense, as centrums, neurapophyses, ribs, &c.; and since they must be distinguished by different special names according to their particular modifications in the same skeleton, as *e. g.* mandible, coracoid, pubis, &c., I call such serially related or repeated parts 'homotypes.' The basioccipital is the homotype of the basi-sphenoid; or in other words, when the basi-occipital is said to repeat in its vertebra or natural segment of the skeleton the basi-sphenoid or body of the parietal vertebra, or the bodies of the atlas and succeeding vertebræ, its *serial homology* is indicated. The study of this kind of homologies was commenced by Vicq d'Azyr, in his ingenious memoir 'On the Parallelism of the Fore and Hind Limbs.' If we except the complex and extremely diversified and modified parts of the radiated appendages of the vertebral segments, to which Vicq d'Azyr restricted his comparisons, the serial homologies of the skeleton are necessarily demonstrated when the general and special homologies have been determined.

In the present section I propose to consider some of those examples of special homology which are least satisfactorily determined and respecting which different opinions still sway different anatomists. Such instances are fortunately few, thanks to the persevering and successful labours of the great comparative anatomists of the last half-century: pre-eminent amongst whom will ever stand the name of CUVIER, in whose classical works, 'Ossemens Fossiles,' 'Histoire des Poissons,' 'Leçons d'Anatomie Comparée' (posthumous edition), and 'Règne Animal,' 1828, will be found the richest illustrations of the special homological relations of the bones in the four classes of vertebrate animals.

Second only to CUVIER must be named GEOFFROY ST. HILAIRE, whose memoir on the Bones of the Skull in Birds as compared with those in Mammals, in the 'Annales du Muséum, t. x. (1807), forms an early and brilliant example of the quest of special homologies, which could not fail, with other and similar investigations of the same ingenious author, to impart a stimulus to that philosophical department of anatomical inquiry[*]. In regard to the osteology of the crocodile, we find Cuvier and Geoffroy engaged in a long parallel series of rival researches, the results of which have had the happiest effects in determining some of the most difficult questions of special homology.

Nor was the co-operation of zealous cultivators of comparative anatomy wanting in the eminent schools and universities of Germany. GOETHE, indeed, had taken the lead in inquiries of this nature in his determination, in 1787, of the special homology of that anterior part of the human upper maxillary bone which is separated by a more or less extensive suture from the rest of the bone in the fœtus; and the philosophical principles propounded in the great poet's famous anatomical essays called forth the valuable labours of the kindred spirits, OKEN, BOJANUS, MECKEL, CARUS, and other eminent cultivators of anatomical philosophy in Germany.

It is not requisite for the purpose I have in view, to trace step by step the progress of the special homological department of anatomy. Its present state, as regards the skull of the Vertebrata, will be best exposed by the view of the fruits of the latest inquiries embodied in TABLE I. appended to this Work.

That table gives at one view the general results of the researches into the conformity of structure of the skull throughout the vertebrate series, by the two great French anatomists who have most advanced this part of osteological science; by the authors of two classical German works on Comparative Anatomy; and by their countryman Dr. Hallmann, who has detailed in an elaborate treatise his especial investigations of some of the most difficult parts of this difficult inquiry. I have added the synonyms of the bones of the head of fishes from the great work of the celebrated Swiss naturalist, who has, so happily for ichthyology, devoted himself to the advancement of that interesting branch of Natural History; and also, the anthropotomical terms for the corresponding parts in the human skeleton. These, after much comparison and deliberation, I have chosen from the justly-celebrated work of SOEMMERRING, the high reputation of which has been sanctioned by the new edition to which some of the most eminent of the German professors of anthropotomy and physiology have recently devoted their combined labours. The English teacher of these sciences will find some of the descriptive designations of the parts by Soemmerring not agreeing with those which he may be in the habit of using, and which are current in the later Manuals of Anthropotomy published in this country: the 'ossa lateralia lingualia' are more commonly called, with us, the 'cornua majora ossis hyoidei'; the 'os spheno-occipitale' is generally described as two distinct bones, the 'os occipitis' and 'os sphenoide'; the 'pars occipitalis stricte sic dicta,' &c. is sometimes called 'squama occipitalis,' or occipital plate; and other synonyms might easily be multiplied from the osteological treatises of Monro and later authors of repute. The fact of such a conflicting and unsettled synonymy still pervading the monographs relating to the human structure, should stimulate the well-wisher to the right progress of anatomy to lend an earnest aid to the establishment of a fixed and determinate nomenclature. A little present labour and the example of adoption, where the reasonableness and necessity of the reform are plain and undeniable, will much accelerate the future progress of anatomical science; and I would respectfully appeal to the Professors and Demonstrators of Human Anatomy for an unbiassed consideration of the advantages of the terms proposed in the first column in Table I. It is designed to express the results of a long series of investigations into the special homologies of the bones of the head, in simple and definite terms, capable of every requisite inflection to express the properties of the parts, and applicable to the same bones from the highest to the lowest of the vertebrate series.

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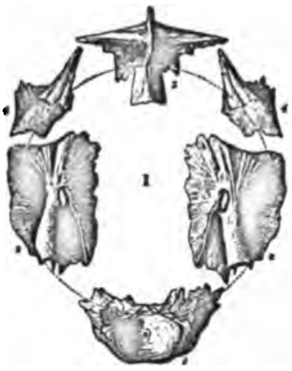
[*] Oken's famous "Programm, Über die Bedeutung der Schädelknochen" was published in the same year (1807) as Geoffroy's Memoir on the Bird's skull; but it is devoted less to the determination of 'special' than of 'general homologies': it has, in fact, a much higher aim than the contemporary publication of the French anatomist, in which we seek in vain for any glimpse of those higher relations of the bones of the skull, the discovery of which has conferred immortality on the name of OKEN.

Apology for Terms.—The degree and extent of the diversity of my determinations from those of other anatomists are shown in the succeeding columns, headed by their names; and I proceed now to give the reasons which have compelled me, in such instances, to dissent from the high authority of Cuvier, Geoffroy, Meckel, Hallmann and Agassiz: these reasons will exonerate me, I trust, from the reproach of underrating their justly-esteemed opinions, which have been abandoned only where nature seemed clearly to refuse her sanction to them. The instances of such dissent are much fewer than they appear to be at first sight. In most cases, where the names differ, the determinations are the same. For 'basilaire,' which Cuvier exclusively applies to the 'pars basilaris' of the occiput, and which Geoffroy as exclusively applies (in birds) to the 'pars basilaris' of the sphenoid, I have substituted the term 'basioccipital' (*basi-occipitale*, Lat.); a term which, as it is more descriptive of the bone in question (1 figs. 1 to 25), will, perhaps, be the more acceptable to those who prefer a determinate to a variable nomenclature, since Cuvier himself has almost as frequently applied to that bone the term 'occipital inférieur' as the term 'basilaire.' For the descriptive phrase 'occipital latéral,' the term 'exoccipital' (*exoccipitale*, Lat.), proposed by Geoffroy, is preferable for the bones 2,2, figs. 1 to 25; especially since the paroccipital is the most 'lateral' of the elements of the occipital bone, in the definite sense in which the term 'lateral' is used in the precise and excellent anatomical nomenclature of Dr. Barclay. For the numerous synonyms borne by the element 3 of the occipital segment of the skull, the term 'supraoccipital' (*supra-occipitale*, Lat.) seemed to best agree with the truest descriptive phrase of the part, viz. 'occipital supérieur.' The interparietal is no constant cranial element, nor is it a dismemberment of one and the same bone of the skull. It is at best only the largest and most common of the accidentally intercalated 'ossa wormiana.' Sometimes, for example, in the *Cebus* monkey, it is a dismemberment of the backwardly-produced frontal bone: more frequently it is the detached upper angle of the supraoccipital. But by this term 'supraoccipital,' I signify the totality of the bone 3 (in figs. 1, 5, 18, 22, 23, 24, 25), confining the term interparietal to its superior and anterior apex when detached, or to the superior and posterior apex of the frontal, when it is in like manner detached and wedged between the parietal bones. The inapplicability of the term 'interparietal' to the whole of the supraoccipital is strongly manifested in those fishes, *e.g.* the carp and tench, in which the supraoccipital is withdrawn from between the parietals to the back part of the skull, leaving those bones to come into contact and unite by the normal sagittal suture on the mesial line of the vertex. Geoffroy's error is of the same kind, and scarcely greater than Cuvier's, where he applies the term 'interparietal' to the whole of the parietal bones in Birds*. The supraoccipital thus defined can never be mistaken for the 'sur-occipital' of Geoffroy, who by this term signifies the elements called 'occipitaux externes' by Cuvier. At the same time the term 'sur-occipital' is too near in sound to 'supraoccipital,' and too significant of the highest part of the occipital segment to be retained for elements, which, like the 'paroccipitals' (fig. 1, 4, 4), are usually inferior in position to the supraoccipital. Geoffroy, moreover, is not consistent in his application of the term 'sur-occipital.' In his memoir on the skull of the crocodile in the 'Annales des Sciences' for 1824, he applies that term to a part of the bone†, the whole of which he calls 'exoccipital' in his later memoir, on the skull of the crocodile, of 1833‡; whilst in the memoir illustrated by the skull of the Sea-perch (*Serranus gigas*) in the 'Annales des Sciences' for 1825, the term 'surroccipital' is applied to the whole of the bones described as 'occipitaux externes' by Cuvier. I trust, therefore, to have shown the necessity for the definite name of 'paroccipital' (*paroccipitale*, Lat.) which is here proposed for the elements, 4, of the occipital segment of the cranium (figs. 1 and 5). The name has reference to the general homology of the bones in question, as 'parapophyses' or transverse processes of the occipital vertebra. And if the purists who are distressed by such harmless hybrids as 'mineralogy,' 'terminology' and 'mam-

Fig. 1.



Disarticulated epencephalic or neur-occipital arch, viewed from behind: Cod (*Morrhua vulgaris*).

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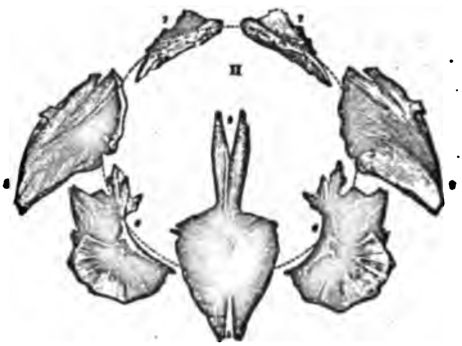
* Annales du Muséum, x. p. 363, pl. 27.

† Pl. 16. fig. 5 s+R. "Plur-occipital formé du sur-occipital et de l'ex-occipital."

‡ Mémoires de l'Acad. Royale des Sciences, t. xii. Atlas, p. 43.

malogy,' should protest against the combination of the Greek prefix to the Latin noun, I can only plead that servility to a particular source of the fluctuating sounds of vocal language is a matter of taste; and that it seems no unreasonable privilege to use such elements as the servants of thought; and, in the interests of science, to combine them, even though they come from different countries, where the required duty is best and most expeditiously performed by such association.

Fig. 2.



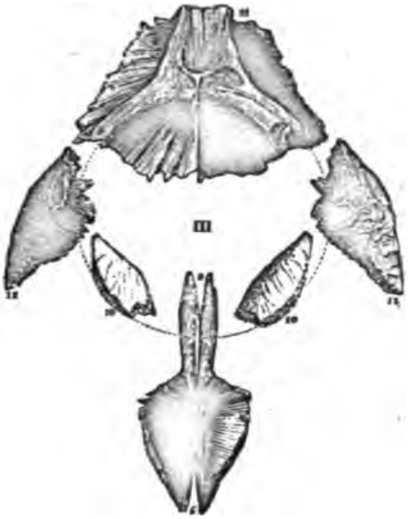
Disarticulated mesencephalic or neuro-parietal arch, viewed from behind: Cod-fish.

For the same motive that suggested the term basi-occipital, viz. because the anthropotomist has been long accustomed to hear that and the corresponding element of the sphenoid bone described as 'basilar processes,' I propose to substitute the term 'basisphenoid' (*basisphenoideum*, Lat.) for the three different descriptive phrases applied to the part (5, figs. 2, 5, 19, &c.) by Cuvier, for the two additional synonyms of Geoffroy, and for the 'sphenoideum basilare' of Hallmann. 'Alisphenoid' (*alisphenoideum*, Lat., 6, 6, figs. 2, 5, 19, &c.) seemed to retain most of the old anthropotomical term of 'alæ majores,' or wings 'par excellence' of the os sphenoideum; as 'orbito-sphenoid' (*orbito-sphenoideum*, 10, 10, figs. 3 and 20) best recalls or expresses the idea conveyed by the descriptive phrase 'alæ orbitales,' or 'ailes orbitaires,' often applied to the homologous bones, regarded as processes of the sphenoid in human anatomy. Here, however, in reference to the alisphenoid, we find the first marked discrepancy in the conclusions of the anatomists who have particularly studied its special homologies. The bone which appears as the 'grande aile du sphénoïde' to Cuvier and Agassiz in fishes, is the 'petrosum' to Hallmann and Wagner; it is also 'rocher' (petrosal) to Cuvier himself in reptiles, and is again 'grande aile du sphénoïde' in birds and mammals. The reasons which have led me to the conclusion that the bones so denominated, as well as the 'ptéreal' and 'prérupeal' of Geoffroy, are homologously one and the same, are so intimately linked with the consideration of the true petrosal and of other elements of the anthropotomist's 'temporal bone,' that I reserve the discussion of these questions until I have completed the apology for the names proposed in the first column of Table I.

The 'parietal' (*parietale*, Lat., 7, 7, figs. 2, 5, 19, &c.) and 'mastoid' (*mastoideum*, Lat., 8, 8, figs. 2, 5, 19, &c.) are amongst the few bones that have had the good fortune to receive, originally, definite names, applicable to them throughout the vertebrate series; although the mastoid, being like the paroccipital, essentially a parapophysis, loses its individuality sooner than do other bones of its segment, and becomes, therefore, a 'processus mastoideus ossis temporis,' in the language of anthropotomy. The homology of the 'parietal' has fortunately been, with a single exception, universally recognised throughout the vertebrate subkingdom; the exception being furnished by the eccentric homologist Geoffroy, who is, as usual, inconsistent with himself, even on this plainest and least mistakeable point.

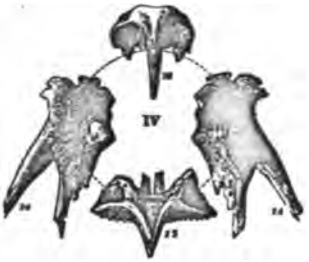
The term 'presphenoid' (*presphenoideum*, Lat. 9, figs. 3, 5, 20, 24, 25, &c.) is proposed for the 'sphénoïde antérieur,' on the principle of substituting, as the better instrument of thought, a definite name for a descriptive phrase. For the same reason 'postfrontal' (*postfrontale*, Lat., 12, 12, figs. 3, 5, 20, &c.) is substituted for Cuvier's 'frontal postérieur' and its synonyms. The 'frontal' (*frontale*, Lat. 11, figs. 3, 5, 20, &c.) and 'vomer' (*vomer*, Lat., 13, figs. 4, 5, 20, 25), are among the few bones which have had their special homologies recognised unanimously throughout the vertebrate sub-kingdom; in the one case even without departure from the original anthropotomical name, and in the other, with but a single deviation from the established nomenclature. But when Geoffroy was induced to reject the term 'vomer' as being applicable only to the peculiar form of the bone in a small proportion of the vertebrata, he appears not to have considered that the old term, in its wider application, would be used without reference to its primary allusion to the ploughshare, and that becoming, as it has, a purely arbitrary term, it is superior and preferable to any partially descriptive one. 'Rhinosphénal,' it is true, recalls the idea of the vomer forming the continuation in the nasal segment of the skull of the basi- and pre-sphenoidal series of bones in other segments; but 'vomer,' used arbitrarily, summons equally every idea derived to form the complex whole from the general study of the bone throughout the vertebrate series.

Fig. 3.



Disarticulated prosencephalic or neuro-frontal arch, viewed from behind: Cod-fish.

Fig. 4.



Disarticulated rhinencephalic, or neuro-nasal arch, viewed from behind: Cod-fish.

'Prefrontal' (*prefrontale*, Lat., 14, 14, figs. 4, 5, 21, &c.) claims the same preference over anterior frontal, and its foreign equivalents, as does postfrontal over its synonymous phrases. There is also another reason for proposing the term; viz. because it is applied to bones in the vertebrate series generally, according to conclusions as to their homological relations, which differ from those to which Cuvier and Geoffroy had arrived. The discussion of the discordant denominations at present applied to this important element of the skull will be fully carried out in the sequel. 'Nasal' (*nasale*, 15, figs. 4, 5, 21, &c.) is another of the few instances in which it is possible to retain and generally apply an old and received anthropotomical term. No one, it is presumed, will contend for the perpetual expression or insertion of the understood generic word 'bone' or '*os*' in this case any more than in the parietal, frontal, &c., which, from being originally specific adjectives, have been properly and conveniently converted into definite nouns.

In conformity with this mode of acquiring an improved as well as brief and precise expression of anatomical facts, I have substituted for 'pars petrosa' or 'os petrosum' the substantive term 'petrosal' (Lat. *petrosum*, figs. 5, 25, 16). The necessity for some such designation for an essentially and often physically distinct bone in the vertebrate skull has been felt by both Cuvier and Geoffroy, when they respectively proposed the names 'rocher' and 'rupéal' for the element in question. 'Petrosal' has appeared to me to be the best English equivalent of Cuvier's 'rocher'; as containing the most characteristic vocable of the old anthropotomical descriptive phrase 'pars petrosa ossis temporis,' &c. 'Rupéal' unfortunately has no determinate meaning: it is applied by its author with certain prefixes to several distinct bones, which already had their proper names. 'Sclerotal' (*sclerotale*, Lat., figs. 5, 22, 23, 17) for 'ossicula seu laminæ osseæ membranæ scleroticæ,' is proposed on the same grounds as exoccipital, postfrontal, &c., viz. the substitution of a name for a phrase. The sclerotals have not been usually included amongst the bones of the head, though they have precisely the same claims to that rank as the petrosals, or other bony capsules of the organs of special sense. Retaining the old anthropotomical term 'ethmoid,' I restrict its application to the very irregular and inconstant developments of bone in the cartilage or membrane which is applied to the anterior outlet of the cranium proper, for the support or defence of the cranial part of the organ of smell. The 'ossa turbinata superiora,' and the 'cellulæ æthmoideæ' are parts of the capsule of that sense, extensively developed in the mammalia, to which the term ethmoid may properly apply; but they must always be distinguished from the modified though constant neurapophyses of the nasal vertebra, called 'prefrontals,' with which the above developments of the olfactory capsule usually coalesce in birds and mammals. 'Turbinal' (*turbinale*, Lat., figs. 5, 25, 19), like petrosal, is a substitute for the phrase 'os turbinatum inferius,' and its synonym 'os spongiosum inferius.'

'Palatine' (*palatinum*, Lat., *ib.* 20) is another of the few fortunate instances of the general recognition of the homologous bone throughout the vertebrate kingdom, with the further advantage of a steady retention of a good old name.

'Maxillary' (*maxilla*, Lat., *ib.* 21) is a similar instance; but Geoffroy, as usual, makes himself singular by adding an uncalled-for synonym. If Soemmerring's term 'mandibula' for the lower jaw were universally adopted and constantly understood to signify the totality of that part of the tympano-mandibular arch throughout the vertebrate series, it would be unnecessary to encumber 'maxilla' with the distinctive epithet 'superior,' which, indeed, expresses a character peculiar only to Man and a few mammalia: in the vertebrate series the 'maxilla' is more commonly anterior than superior to the 'mandibula.'

I have adopted the term 'premaxillary' (*premaxillare*, Lat. *ib.* 22), as used by M. de Blainville and some other distinguished continental osteologists, in preference to 'intermaxillary;' because that term has already been applied (by Schneider) to another bone of the skull (the tympanic in birds), of which it is more accurately descriptive, than it is of a bone which is more commonly before than between the maxillary bones. 'Entopterygoid' (*entopterygoideum*, Lat.) claims preference to the phrases 'ptérygoïde interne' of Cuvier and Agassiz, on the same logical grounds as have already been urged in favour of 'exoccipital,' 'prefrontal,' &c. But I have also another reason for proposing a definite term for the bone 23, fig. 5, which I regard as a peculiarly ichthyic development. Cuvier has applied the term 'ptérygoïde interne' to another part of the diverging appendage of the palato-maxillary arch, which part, I concur with Dr. Köstlin in regarding as homologically distinct from the 'entopterygoid' of fishes. For the part in question, viz. the 'os transverse' of Cuvier in the skull of fishes (24, fig. 5), and its homologue in reptiles, which he calls 'ptérygoïdien interne' (24, fig. 22), I retain the term 'pterygoid' (*pterygoideum*, Lat.), meaning pterygoid proper: and to the bone which Cuvier calls 'transverse' in reptiles (24', fig. 22), I apply the term 'ectopterygoid' (*ectopterygoideum*, Lat.); but this, as the table demonstrates, does not signify Cuvier's 'os transverse' in the skull of fishes. Entopterygoid, pterygoid and ectopterygoid, have, therefore, both the advantages of substantive terms, and of being applied steadily each to a distinct bony element. The 'hérisséal' of Geoffroy, like the 'ptérygoïde interne' of Cuvier, means one thing in a fish and another in a crocodile; Geoffroy has also encumbered the latter bone with a third synonym. 'Malar' (*malare* or *os malæ*, Lat.) is preferable to 'jugal,' because Cuvier applies that name to one bone in a fish, to another in a mammal, and to two essentially distinct though coalesced bones in a bird. Malar is also the name most commonly applied by English anthropotomists to the bone, to the true homologue of which I would restrict its application throughout the vertebrate series.

With regard to the 'squamosal' (*squamosum*, Lat. pars squamosa, &c., figs. 22–25, 27), it may be asked why the term 'temporal' might not have been retained for this bone. I reply, because that term has long been, and is now universally, understood in human anatomy to signify a peculiarly anthropotomical coalesced congeries of bones which includes the 'squamosal' together with the 'petrosal,' the 'tympanic,' the 'mastoid,' and the 'stylohyal.' It seems preferable, therefore, to restrict the signification of the term 'temporal' to the whole (in Man) of which the 'squamosal' is a part. To this part Cuvier has unfortunately applied the term 'temporal' in one class and 'jugal' in another: and he has also transferred the term 'temporal' to a third equally distinct bone in fishes; whilst to increase the confusion, M. Agassiz has shifted the name to a fourth different bone in the skull of fishes. Whatever, therefore, may be the value assigned to the arguments which will be presently set forth, as to the special homologies of the 'pars squamosa ossis temporis,' I have felt compelled to express the conclusion by a definite term, and, in the present instance, have selected that which recalls best the accepted anthropotomical designation of the part, although 'squamosal' must be understood and applied in an arbitrary sense, and not as descriptive of a scale-like form, which, in reference to the bone so called, is rather its exceptional than normal figure in the vertebrate series.

The term 'tympanic' (*tympanicum*, Lat.) appears to have received the most general acceptance as applied to that bone which the early ornithotomists have called 'os quadratum' and 'os intermaxillare,' (fig. 23, 28) and which as a process of the human temporal, sometimes called 'external auditory,' supports the tympanic membrane (fig. 25, 28). 'Caisse' is the French and 'pauke' the German equivalent; but Cuvier more commonly uses the phrase 'os tympanique.' The chief point, in reference to that term, as applied by Cuvier, from which I find myself compelled to dissent from the great and ever-to-be-revered anatomist, relates to the view which he has taken of the large and long pedicle which supports the mandible in fishes, and which, in that class, is subdivided into sometimes two, sometimes three, and commonly into four pieces. I regard this subdivision of the elongated supporting pedicle as explicable chiefly, if not solely, by reference to a final purpose, viz. to combine strength with a certain elastic yielding and power of recovery, in the constant and powerful movements to which it is subject in the transmission of the respiratory currents, and in the prehension and deglutition of the food. Cuvier himself regards in the same light the analogous subdivision of the mandibular or lower half of the arch, and both Conybeare* and Buckland† have well illustrated the final purpose which the subdivision of the lower jaw of the Crocodile into overlapping pieces, subserves. Cuvier has given distinct and convenient names to these several pieces of the mandible, but he views them collectively as answering to the simple mandible of the mammal and the bird. I, in like manner, regard the subdivided pedicle supporting the mandible in fishes as answering to the undivided pedicle supporting the mandible in ophidians, lizards and birds. There is the same necessity or convenience for a distinct name to each distinct part of the tympanic pedicle, or upper part of the tympano-mandibular arch, as for the divisions of the mandible or lower part of that arch. But Cuvier unfortunately persuaded himself that the subdivisions of the tympanic pedicle in fishes represented other bones in higher vertebrates besides the tympanic, and applied to them the names of such bones. I have been compelled, therefore, in dissenting from this view to propose new names for the peculiar ichthyic subdivisions of the tympanic, and in doing so I have been careful to retain the dominant term, and to distinguish the parts by prefixes indicative of their relative position. Time and the judgement of succeeding homologists will determine the accuracy or otherwise of this view; and, should it be ultimately adopted, I feel great confidence that the terms 'epitympanic' (*epitympanicum*, Lat., fig. 5, 28a), mesotympanic (*mesotympanicum*, 28b), pretympanic (*pretympanicum*, 28c) and hypotympanic (*hypotympanicum*, 28d), will be preferred to the names proposed by Geoffroy St. Hilaire for the same parts. With regard to the subdivisions of the mandible in cold-blooded vertebrates, I adopt most of those proposed by Cuvier. As, however, 'operculaire' had been applied by the great anatomist to a distinct bone in fishes, it was necessary, in order to avoid its use in a double sense, to substitute a distinct name for the part of the jaw in question, and as it is always applied, like a surgeon's splint or plaster to the inner side of most of the other pieces, that of 'splenial' (*splenium*, Lat., figs. 22, 23, 31) suggested itself to me as the most appropriate name. For an obvious reason I have restored the term 'coronoid' (*coronoideum*, 31') in place of 'complementary,' for the piece into which the crotaphite muscle is always more or less inserted in the mandible of reptiles. There is no ground for disturbing the appropriate names given by Cuvier to the parts of the diverging appendage of the tympano-mandibular arch in fishes; and the same principle which he has adopted in distinguishing the different opercular bones (fig. 5, 34–37), has guided me in naming the different parts of the bony pedicle which supports them.

I have gladly adopted as many of the well-devised terms which Geoffroy proposed for the elements of the hyoid arch, as his unsteadiness in their application would permit to be retained. They are obviously preferable to the descriptive phrases by which Cuvier designates the homologous parts.

The substantive terms applied to the corresponding divisions of the branchial arches have been modelled on those of the hyoid system; but I have deviated in one instance from the rule which has governed throughout my nomenclature of the bones, in proposing a second name for a modified homologue in the air-breathing animals, of a part of the branchial apparatus in fishes, viz. that part which is retained even in the human hyoid, and which is known in anthropotomy as the 'os laterale linguale,' or 'cornu majus ossis hyoidei;' for this part I have proposed the name 'thyrohyal,' for the reasons assigned in the note (2) to Table I.

The names assigned to the bones of the scapular arch (figs. 5, 22, 23, 24, 25,

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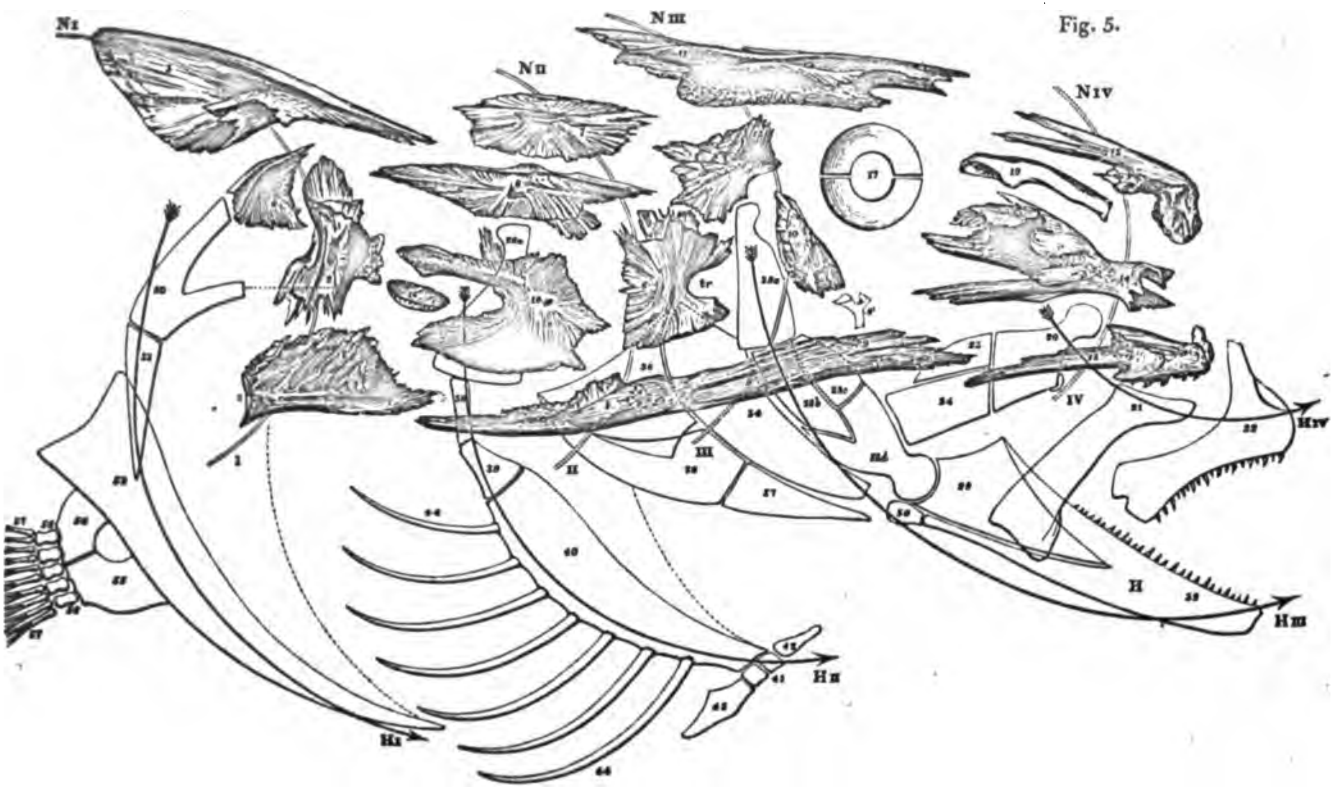
* Geol. Trans., vol. v. p. 563. † Bridgewater Treatise, vol. i. p. 176.

23, *50–52*) and its appendages (*ib.* *53–58*) agree so closely with those which they have always borne as to require no explanation here. The chief surprise of the anthropotomist will be occasioned by their being included amongst the bones of the head. That the upper or pectoral extremity and its supporting arch form actually parts of the integral occipital segment of the skull, will be proved in the memoir on the general homologies of the bones of the head. I may, here, however, in reference to the terms 'ulna' and 'radius,' request the anatomist to compare the skeletons of the perch or cod with that of the porpoise. The pectoral extremity is in the form of a fin, and in both fish and marine mammal it is applied, in a state of rest, prone to the side of the trunk; in this position it will be seen in the *Delphinus*, that the radius is downward, and the ulna with its projecting olecranon upwards. I take this as the guide to the homology of the two bones that support the carpal series of the pectoral fin in fishes. Cuvier, however, gives the name of 'cubital,' perhaps on account of its angular olecranoid prolongation, to the lower bone, and 'radial' to the upper bone: and in these determinations he is followed by M. Agassiz. Both bones coalesce with the supporting arch in the lophius and some other fishes; and since, in the lophius, two of the carpal bones are unusually elongated, Geoffroy mistook these for homologues of the radius and ulna. The condition of the pelvic member or ventral fin is, in fact, here repeated in the pectoral; there being no homologous segment of thigh or leg interposed in any ventrals between the supporting (pelvic) arch and the fin-rays representing the tarso-metatarse and phalanges. The earlier stages in the development of all locomotive extremities are permanently retained or represented in the paired fins of fishes. First the essential part of the member, the hand or foot, appears: then the fore-arm or leg; both much shortened, flattened and expanded, as in all fins and all embryonic rudiments of limbs: finally comes the humeral and femoral segments; but this stage I have not found attained in any fish. It is with considerable doubt that I place, qualified by a note of interrogation, Cuvier's "troisième os qui porte la nagoire pectorale" as the homologue or rudimental representative of a 'humerus.' Normally, I believe this proximal member of the radiated appendage of the scapular arch not to be distinctly eliminated from that arch in the class of fishes. The Siluroids are examples of a similar confluence of the first segment (preoperculum) of the diverging appendage of the tympanic arch with that arch. With regard to the lower, distal or apical element of the scapulo-coracoid arch, always the largest bone of the arch in fishes, Cuvier's idea that it is the 'humerus,' far less accords with the law of the development, the connections, and the essential nature of that bone, than the more prevalent view, that it represents the clavicle: a view entertained by Spix, Meckel, and Agassiz, by Wagner, who calls it 'vordere Schlüsselbein,' and by Geoffroy, who calls it 'furculaire.' I have, however, been induced to regard the lower element of the scapular arch, in fishes (fig. *5*, *52*), as homologous with that bone, the 'coracoid,' which progressively acquires a more constant and larger development in descending from mammals to fishes, and which is manifestly a more essential part of the arch than the clavicle, since it is more constant in its existence, and always more completely developed in birds and reptiles; and especially since it contributes more or less of the surface of attachment for the radiated appendage, which the clavicle never does. With reference, also, to the Cuvierian determination of the hæmapophysial portion of the occipital inverted arch in fishes, this is unquestionably as essential an element of the arch as is the 'coracoïde' in other vertebrates; and it is the most important part in the piscine class, in no member of which does it present the slightest approach to the character of

Fig. 5.



Disarticulated bones of the neural arches (N I to IV) and sense-capsules; the hæmal arches (H I to IV) and appendages in diagrammatic outline. Cod (*Morrhua vulgaris*).

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a diverging appendage, such as the humerus essentially is, whenever it has an independent existence. By some ichthyotomists, the bone which I call coracoid (52) has received the special name of 'cœnosteon.'

Cuvier's usual judgement and acumen seem to have been in abeyance, when, having determined the rays of the pectoral fin to represent the bones of the hand, and the two bones which support them in fishes to be those of the fore-arm, he concluded that, therefore, the great bone which completed the scapular arch "répondra donc nécessairement à l'humérus."—*Hist. des Poissons*, 4to. i. p. 274. The great anatomist assigns no other reason: but the arch supporting the ventral fin does not necessarily answer to the tibia or the femur, because neither of these segments are interposed between the arch and its appendage—the modified foot. The scapula of many reptiles, especially of the batrachia, is manifestly, he proceeds to state, composed of two bones. But in those reptiles the arch is completed below by a third bone, which neither Cuvier nor any other anatomist has called 'humerus.' Now Cuvier's 'humerale' in fishes precisely answers to that third bone in reptiles which he rightly calls the 'coracoid' in that class.

The coracoid of fishes being thus determined, it necessarily follows that that inconstant bone, or pair of bones (58) posterior to it on each side, cannot be, as Cuvier, Geoffroy, Meckel and Agassiz have supposed, the representative of the 'os coracoïdien' of the reptile and bird. It holds, indeed, as they have said, the same relative position to the bone 52, here called coracoid, which the coracoid in the lizard and bird holds to the clavicle in those animals. But is no account to be taken of the remarkably though normally advanced position of the scapulo-coracoid arch in fishes? Granting, as I shall give evidence to prove in treating of the general homologies of the bones, that the bone (58) called by Cuvier 'coracoïdien' in fishes appertains to a vertebral segment posterior to the occipital one, yet in the extraordinary backward displacement which the true scapulo-coracoid arch undergoes in the air-breathing vertebrates, may not the relative position of 58 to that arch become reversed, and the part which is behind in fishes become before in birds? I entertain no unmeet confidence in the correctness of my view of the special homology of Cuvier's 'os coracoïdien' in fishes with the furculum or 'clavicle' (fig. 25, 52') of air-breathing vertebrates: the argument against such a view, from its posterior position in fishes, has not, however, the same weight with me as it appears to have had with Cuvier and his followers: and, leaving this as one of the undecided points in special homology, with the proposition of the provisional name of 'epicoracoid' (*epicoracoideum*, Lat.) for the piscine bone in question, I proceed to consider other unsettled points of special homology, for the determination of which there are better and surer grounds.

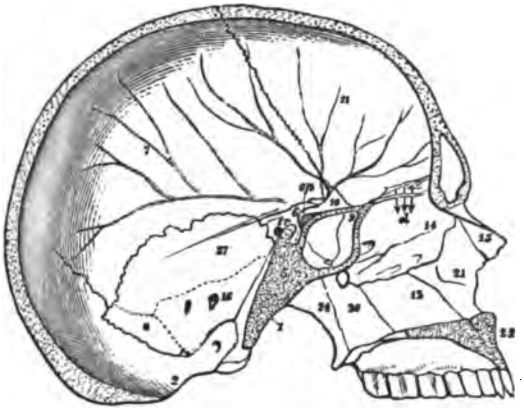
Moot Cases of Special Homology.—The first discrepancy, demanding particular consideration, which meets the eye in the TABLE I. is that which relates to the determination of no. 6. The German authorities regard what I believe to be the homologue of the human 'ala major sphenoidalis' in the cold-blooded Vertebrata, to be the homologue of the 'pars petrosa ossis temporis.' Cuvier rightly recognises the 'grande aile du sphénoïde' in mammals, birds and fishes, but regards my 'alisphenoid' in reptiles as the 'rocher' or 'pars petrosa.' Geoffroy concurs with Cuvier and the German anatomists so far as to view my 'alisphenoid' in the Crocodile as a dismemberment of the petrosal, calling it 'prérupéal;' but he recognises, like Agassiz and Cuvier, the true alisphenoid in fishes, and with them differs in that respect from the German homologists. It does not appear that the alisphenoid has been mistaken for any other bone than the petrosal, and the question to be determined, therefore, is, What are the essential characters respectively of the 'alisphenoid' and the 'petrosal' in the vertebrate series?

Those of the *alisphenoid* appear to me to be the following:—1st, its connection below with the basisphenoid and behind with the petrosal, where it forms the forepart of the 'otocrane' or cavity for the reception of that osseous or cartilaginous immediate capsule of the labyrinth or internal organ of hearing: the alisphenoid is also commonly, but not constantly, joined before with the orbitosphenoid, and above with the parietal: it has other less constant connections with the squamosal, the exoccipital, the supraoccipital and the basioccipital: 2ndly, with regard to its essential functions, the alisphenoid protects more or less of the side of the mesencephalon, or (in mammals) of the middle lobe of the cerebral hemisphere: it gives exit, by notches or foramina, to the third, and usually, also, to the second divisions of the trigeminal or fifth pair of nerves.

The essential character of the *petrosal* is to envelope immediately the whole of the vascular and nervous tunics of the labyrinth or internal organs of hearing, either in a membranous, a cartilaginous or an osseous state; its histological condition being much less constant than that of the alisphenoid.

On viewing the alisphenoid on the interior surface of the human skull (fig. 6, 6), it seems to be the least significant and important part of the lateral walls of the cranial cavity: it forms their smallest portion: it is much surpassed in extent by the squamosal (*ib.* 27) and the supra-occipital (*ib.* 3), and still more so by the enormously expanded parietal (7) and frontal (11). Nevertheless we find it connected, anchylosed indeed, below to the basisphenoid (5), bounding anteriorly the space into which the petrosal (16) is wedged; connected in front with the orbito-sphenoid (10), and usually articulating by its superior apex with the parietal: I purposely omit the mention of other connections of the alisphenoid in Man which are less constant in the vertebrate series. But it is important to observe, notwithstanding the displacement which the alisphenoid has undergone through the intercalation of the extraordinarily developed squamosal into the lateral walls

Fig. 6.

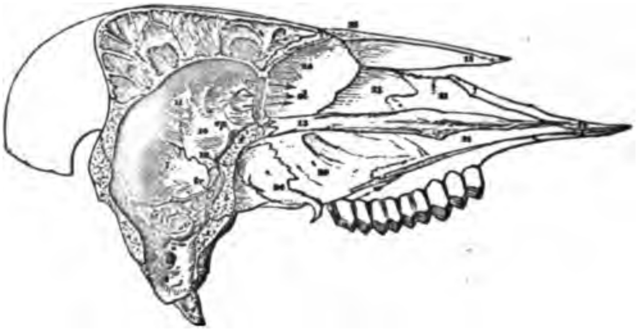


Vertical longitudinal section of the human cranium.

of the cranium, that it is still perforated by the third (*ib.* *tr*) and second divisions of the fifth or trigeminal nerve.

In tracing the alisphenoid downwards through the mammalian series, we cannot but be impressed with the conviction of its true character and importance as an essential part of the cranium, from its constancy in the formation of its walls, and by observing that, whilst the share which the squamosal takes in them progressively decreases,—until in the sheep, for example, it is quite excluded from the cranial cavity,—that of the alisphenoid (fig. 7, 6) increases as the cavity itself diminishes in size; and, further, that this increase is not accompanied with any material change in the relative size of the alisphenoid to the basisphenoid. The share which the alisphenoid takes in forming the anterior boundary of the otocrane increases; as does also the extent of its superior connections, especially of that with the parietal (7). It is important, in tracing these modifications, to note, also, the change in the relative position of the foramen ovale in the mammalian series. In Man the foramen ovale (fig. 6, *tr*) is close to the hinder border of the alisphenoid; and in some quadrumanes the third division of the fifth escapes through a notch in the same border. This position of the foramen ovale relates to the alisphenoid being pushed forward by the intrusion not only of a large ossified petrosal (16), but of a still larger squamosal (27). In the sheep, however, the foramen ovale is no longer at the posterior margin; but, the alisphenoid, having retrograded by the recession of the squamosal towards its more normal exterior position in the vertebrate series, the third division of the trigeminal now perforates its middle part (fig. 7, *tr*). It may be observed that, concomitantly with this retrogradation of the alisphenoid, the orbito-sphenoid (*ib.* 10) acquires larger proportional dimensions than in Man (fig. 6, 10).

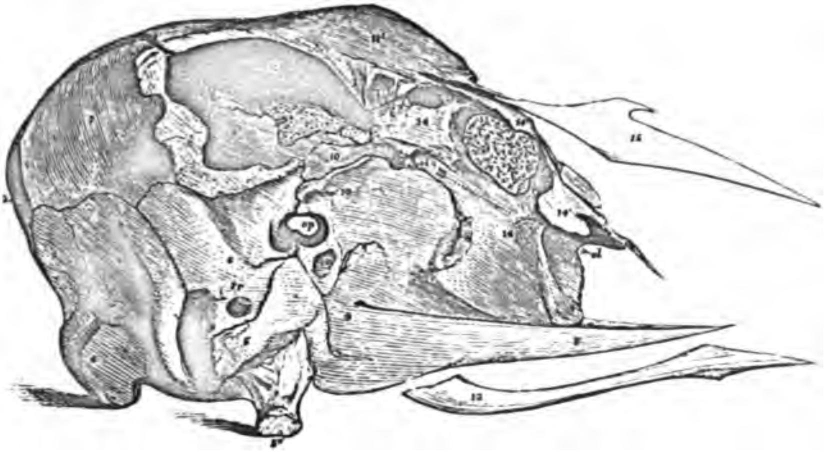
Fig. 7.



Vertical longitudinal section of the cranium of a sheep (*Ovis Aries*).

In the bird the alisphenoid (fig. 8, 6) is recognizable by the repetition of the connections which it presented in the sheep; the squamosal being quite excluded from the cranial parietes, and, indeed, never again presenting itself in the capacity of a cranial bone in any of the oviparous vertebrates. The alisphenoid (fig. 23, 6) is in contact posteriorly with the petrosal (*ib.* 16), which soon becomes anchylosed with it, as well as with the exoccipital (2), mastoid (8), and other bones forming the cavity for the reception of the ear-capsule, in all birds. The alisphenoid further manifests its true homology in the bird by its other constant character of transmitting the third and also the second or maxillary division of the trigeminal nerve; which divisions, in the

Fig. 8.

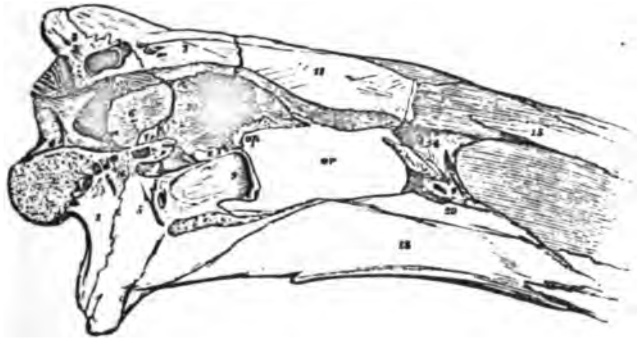


Partly disarticulated cranium of a young ostrich (*Struthio camelus*), natural size.

young ostrich, I found distinctly perforating the middle of its lower border (fig. 8, 6, *tr*). The alisphenoid is deeply impressed by the chief ganglions of the mesencephalon, viz. the optic lobes. The prosencephalon or hemispheres are still defended principally by expanded parietals (*ib.* 7) and frontals (*ib.* 11)*.

In the crocodile these spines of cranial vertebræ are much restricted in their development, and a larger proportion of the hemispheres is defended by the orbitosphenoid (fig. 9, 10), which here surpasses the alisphenoid (*ib.* 6) in size. This, however, still performs its essential and characteristic functions of protecting the sides of the mesencephalon, and giving issue to the chief part of the trigeminal nerve. Owing to the diminution in size of the

Fig. 9.



Vertical longitudinal section of the cranium of a crocodile (*Crocodilus acutus*).

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* The right frontal has been removed to show better the extent and connections of the orbitosphenoid (10) and the prefrontal (14).

petrosal (16), and the retention by a great proportion of this capsule of the acoustic labyrinth of its primitive cartilaginous state, it occupies a smaller interval between the alisphenoid (6) and exoccipital (2). It no longer protrudes as a large bony wedge (as in figs. 6 and 7, 16) into the cranial cavity, but permits the alisphenoid to come into connection with the exoccipital. The result of this further retrogradation of the alisphenoid, in regard to the relative position of the outlet of the third division of the fifth, is analogous to that which occurs in the sheep. We saw in that mammal, through the recession of the squamosal, the foramen ovale advanced from the posterior to the middle part of the alisphenoid; in the crocodile, through the further removal from the cranial cavity of the interposed petrosal, the foramen ovale is advanced to the anterior border of the alisphenoid; which border, in fact, it notches, the nerve escaping by a common foramen or 'trou du conjugaison' between the alisphenoid and the orbitosphenoid, the hole, however, being principally formed by the alisphenoid (fig. 9, *tr*). This position of the 'foramen ovale' loses all its value as an argument in favour of the petrosal character of no. 6, by analogy with the position of the foramen ovale in man or the ape, when we take into consideration the necessary consequences of the successive withdrawal of the squamosal and true petrosal from the inner surface of the cranium in descending to the reptiles. The orbitosphenoid (fig. 9, 10), notwithstanding its great relative size, retains all its essential characters: it is perforated or notched for the exit of the optic nerves (*op*) and first division of the fifth pair (*5*); it rests upon the presphenoid (9) below, and likewise, through its backward development, partly upon the basisphenoid, and it articulates with the frontal (11) above, and also through the same backward extension with the parietal (7); it constitutes the anterior border of the lateral bony parietes of the cranium, which are interrupted by the orbits, and separated by their interposition in saurians and fishes from the rhinencephalic part of the cranial cavity (at 14, fig. 9). The characters, in fact, of the orbitosphenoid are so clearly manifested in the crocodile, that Cuvier, having been led by the increased share, as compared with mammals, which the crocodile's alisphenoid (fig. 9, 6) takes in the formation of the otocrane, to regard it as the petrosal, and yet perceiving the essential characters of the orbitosphenoid in the bone (*ib.* 10) anterior to it, was driven to the conclusion that that bone represented both orbitosphenoid ('aile orbitaire du sphénoïde') and alisphenoid (aile temporale du sphénoïde). The cold-blooded crocodile, however, is not exactly the animal in which we should expect to find so unusual an instance of obliteration of sutures, as that between the alisphenoid and orbitosphenoid*. The actual and most characteristic modification of the orbitosphenoid in the crocodile's skull, is its retrogradation together with the alisphenoid, or rather the maintenance of its normal connection therewith by increased antero-posterior development, whereby it comes into communication above with the parietal (7) and below with the basisphenoid (5); whilst the alisphenoid, in like manner, gains a connection with the supra-occipital (3) above and the basi-occipital (1) below; although it still retains its more normal relations with the parietal, and rests in great part on the basisphenoid (5), as the orbitosphenoid rests in great part upon the pre-sphenoid (9.) The superior connections of the orbitosphenoid and alisphenoid are always less constant than their inferior ones. By these latter characters, and still better by their nerve-outlets and their relations to the primary divisions of the encephalon, are they rightly and truly determinable. The German authors who have followed Cuvier in his views of the special homology of the alisphenoid in reptiles, are more consistent than the great French anatomist in regard to the alisphenoid of fishes. Dr. Hallmann, accepting Cuvier's characters of the petrosal, taken from its internal position and lodgement of the whole or part of the labyrinth*, naturally applies them to the alisphenoid in fishes, and adds to the grounds for regarding that bone as the 'petrosal,' that it is in some fishes perforated by the opercular branch of the great trigeminal nerve†. But, admitting the homology of the opercular nerve with the facial nerve of mammals, yet its wider homology and essential character as a motor division of the great trigeminal nerve must not be lost sight of: its origin in close contiguity with the great sensory portions of the trigeminal in fishes accords better with the character of that nerve as the great spinal nerve of the brain, than it usually presents in higher classes; and it is surely no important departure of the alisphenoid from its normal character, that it should give exit to both motory and sensory divisions of the great nerve with which it is so intimately associated from man down to the fish. Indeed, the progressive withdrawal of the bony petrosal from the interior of the skull and the concomitant backward extension or retrogradation of the alisphenoid, ought to prepare us to expect that nerves which traverse the petrosal in mammals should perforate the alisphenoid in reptiles and fishes. And so we find in the carp that the glosso-pharyngeal even perforates the posterior border of the alisphenoid; but its origin close to the acoustic and facial nerves in fishes diminishes the force of the argument which might be drawn from this exceptional perforation in favour of the petrosal character of the alisphenoid. I concur entirely with Cuvier and M. Agassiz in their determination of the alisphenoid in fishes; but, if the great share which that bone in reptiles (figs. 9 and 10, 6) contributes to the formation of the otocrane, if the anterior position of the foramen ovale, and the superior connection of the bone with the supra-occipital, are proofs (as Cuvier believed) of its homology with the petrosal in the class *Reptilia*, they ought also, as Hallmann and Wagner contend, to establish the same special homology of the bone (fig. 5, 6) in the class *Pisces*. But none of these are essential characters of the petrosal. The petrosal is a *contentum* and not a *paries*, or any part of the parietes of the otocrane or cranial chamber lodging the organ of hearing: it is the outermost tunic, membranous, gristly, or bony, of the labyrinth or essential part of the acoustic organ. Had the above-cited anatomists clearly appreciated the general homology of the petrosal, they could scarcely have failed to detect its special homologies in the vertebrate series. Cuvier was evidently guided to the true determination of the alisphenoid in fishes, less by its own essential characters, than by observing in certain fishes, the perch and cod for example, a partial ossification of the acoustic capsule, to which, therefore, he assigned the name 'rocher.' And, having thus satisfied himself of the existence of the homologue of the 'pars petrosa,' &c., he could not but assign to the bone which rested below upon the basisphenoid, which protected laterally the optic lobes and gave exit to the third division of the trigeminal nerve, the name of 'grande aile du sphénoïde.' But all these characters equally coexist in the bone which Cuvier calls 'rocher' (petrosal) in the crocodile and other reptilia. He was not aware, however, that in both gavials and crocodiles a distinct ossicle, the veritable homologue of the intra-cranial pyramidal-shaped petrosal of mammals and birds, makes its appearance between the alisphenoid, exoccipital and basioccipital, as at 16, fig. 9. Here, however, it is necessary to offer a few observations on the sense in which I use the term 'petrosal' as applied to that ossicle.

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* No one better appreciated the characteristic persistence of the sutures in the crocodile than Cuvier, when his attention was not diverted from it by a favourite hypothesis. "Le crocodile a cela d'avantageux à l'étude de son ostéologie, que ses sutures ne s'effacent point, du moins n'en a-t-il disparu aucune dans nos plus vieilles têtes," is the remark with which he commences his article on the determination of the bones of the head of that reptile (Ossemens Fossiles, 4to. v. pt. ii. p. 69): but at p. 76, a suture is assumed to be effaced, which is present in most mammals and all cold-blooded vertebrates, where a wider space does not intervene between the alisphenoid and orbitosphenoid.

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* Ossemens Fossiles, 4to, t. v. pt. i. p. 81.

† Der vergleichende Osteologie des Schläfenbeins, p. 64.

The petrosal, properly so called, considered in its totality, as the immediately investing capsule of the labyrinth or internal organ of hearing, is wholly cartilaginous in many fishes and saurians, and in all batrachians, ophidians and chelonians, and is contained in a cavity or orbit (otocrane) which most, or all of the elements of the occipital and parietal vertebræ concur in forming. A part of the ear-capsule remains cartilaginous in the crocodile; but several portions become ossified around the semicircular canals and rudimental cochlea, which ossifications contract slender adhesions to the smooth otocranial surfaces of the supraoccipital, exoccipital and alisphenoid; and to one of these portions (on the principle on which Cuvier applies the term 'rocher' in fishes) the name petrosal might more particularly be given, as it is more distinct and moveable than the other partial ossifications of the capsule, and contributes to form the 'meatus internus' towards the cranial cavity, surrounds nearly the whole of the 'fenestra rotunda', and one-half of the 'fenestra ovalis' towards the tympanic cavity. Looking upon the inner surface of the lateral walls of the cranium (as at fig. 9), one sees at the bottom of the T-shaped suture* uniting the otocranial laminæ of the exoccipital, alisphenoid, and supraoccipital bones, a fourth osseous element (16), presenting a convex extremity towards the cranial cavity, and completing, with the exoccipital, the lower half of the foramen for the nervus vagus. If this little bone be pressed upon with a needle or probe, it yields and moves, being divided by smooth harmoniæ from both the exoccipital (2) and alisphenoid (6).

The protuberance in question, which thus projects into the cranial cavity, is the rounded angle of the border of the inferior plate of the petrosal, which joins the exoccipital. This lower horizontal plate of the petrosal forms the upper wall of the 'fissura lacera posterior,' and the lower wall of the 'fenestra cochleæ': the fore-part of the horizontal plate bends upwards, twisting and expanding into a vertical oval plate, articulated by its anterior surface to a corresponding sutural surface of the alisphenoid. The lower margin of this plate forms the upper boundary of the 'fenestra cochleæ,' and is continued into a thin plate of bone which divides the 'fenestra cochleæ' from the 'fenestra vestibuli' above. This thin plate of the petrosal joins and is usually anchylosed to the exoccipital: it is the only part of the true petrosal noticed by Cuvier, who describes it as a slender filament of bone which separates the two fenestræ†. Seen edgewise, looking into the tympanic cavity, the plate appears like a filament: and this plate forms the sole connection, when any exists, between the petrosal and the exoccipital. I have always found the sutures persistent between the petrosal and the alisphenoid. The upper border of the 'fenestra vestibuli' is formed by a petrosal, or rather otocranial, process of the alisphenoid.

The part (fig. 9, 16) entering into the formation of the lateral walls of the brain-case, and which is here specially indicated by the name of 'petrosal,' seems to have been overlooked: it is, however, relatively to the alisphenoid or exoccipital, as large as is the petrosal (Cuvier's rocher) in the perch: it has a true osseous texture, and is quite distinct from the lenticular mass of calcareous matter in the adjacent cochlear chamber which Cuvier compares to starch ('amidon durci').

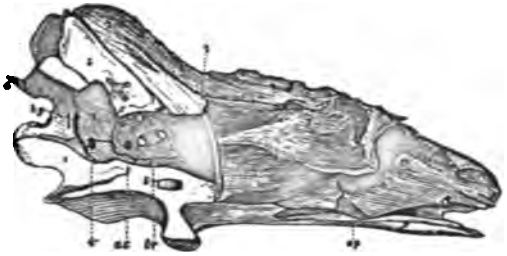
* Suture à trois branches, Cuvier, *l. c.* p. 165.

† Du côté de la caisse la paroi est percée de deux fenêtres transversalement oblongues et séparées par un filet mince." *l. c.* p. 82.

Neither the figure of the interior surface of the cranium of the crocodile, which Spix gives as that of the Nilotic species in his great 'Cephalogenesis,' tab. ii. fig. 6; nor the figure given by Geoffroy of the skull of his *Crocodilus suchus* in the 'Annales des Sciences,' tom. iii. pl. 16, fig. 2; nor that of the *Crocodilus biporcatus*, which illustrates the later memoir by the same author in the 'Mémoires de l'Académie Royale des Sciences,' t. xii. (1833), pl. 1, fig. 2.; nor that (if it be an original figure) published by Dr. Hallmann in his 'Comparative Anatomy of the Temporal Bone' (taf. iii. fig. 49), give any indication of this, in the determination of the homology of the alisphenoid and petrosal, most significant and important ossicle. The proof of its normal character will be afforded by comparisons of the description and figure of the part here given with a section of the cranium of any true *Crocodilus*, *Alligator* or *Gavial*. In the latter, the otocranial plates of the alisphenoid, exoccipital and supra-occipital, project considerably into the cranial cavity. Any one of these plates might be called 'petrosal,' for such reasons as have induced Cuvier to apply that name to the alisphenoid in the crocodile and other reptiles*. We find, indeed, that Geoffroy has applied the equivalent term, by turns, to each. But the true idea of the petrosal should include all those gristly and bony parts of the immediately investing capsule of the labyrinth which occupy the otocranial excavations of the exoccipital, supraoccipital and alisphenoid; and as the ossified portions of the true petrosal, in the crocodile, usually contract a bony union with the parietes of the otocrane, all these bony portions of the immediate capsule of the labyrinth might be called 'petrosal processes' of the bones to which they respectively adhere. That portion which unites to the exoccipital is attached by two lamellæ; it forms a great part of the cochlear cavity, the lower half of the posterior semicircular canal and the hinder half of the external or upper semicircular canals: that plate which belongs to the supra-occipital is attached to its otocranial surface by three points, and forms the upper third part of the anterior semicircular canal and the crus of the posterior canal which communicates therewith: that part which adheres to the alisphenoid forms the anterior crus of the anterior (in Man superior) semicircular canal and the anterior beginning of the external canal. The proper and usually distinct bony portion of the petrosal (fig. 9, 16), which articulates with both alisphenoid and exoccipital, forms part of the 'meatus internus,' nearly the whole of the 'fenestra cochleæ,' and half of the 'fenestra vestibuli': it can only be regarded a 'petrosal process' of the exoccipital by virtue of the very limited anchylosis occasionally contracted by the thin plate dividing the two 'fenestræ,' along with the true petrosal process of the exoccipital above described.

If we compare with the inner wall of the crocodile's cranium that of an ophidian, the python for example (fig. 10), we shall find the walls of the 'otocrane' or chamber of the labyrinth to be contributed by the exoccipital, (2) supra-occipital (3) and alisphenoid (6) in nearly equal proportions; the basioccipital (1), also, being ac-

Fig. 10.



Cranium of a python partially bisected. Natural size.

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* Ossemens Fossiles, 4to. 1824, v. ii. pp. 81, 180, 258.

cessory to the formation of the floor of the ear-chamber: the three principal bones are united, as in the crocodile, by a triradiate suture. The petrosal, which, like the squamosal, was gradually more and more withdrawn and shut out from the cranial cavity, as we decended from mammals, now entirely disappears from view: and it retains its primitive cartilaginous state in serpents as it does in chelonians, lizards and batrachians. The essential characters of the exoccipital (2) are manifested by its relative position and connections; by its affording exit for the vagal (*v*) and hypoglossal (*hy*) nerves, and by its protecting the sides of the epencephalon. The alisphenoid (6) is not less clearly indicated by its constant and essential characters; it rests below upon the basisphenoid (5), it articulates above with the parietal (7), and behind with the cartilaginous petrosal; but the otocranial plate being, as in the crocodile, unusually extended backwards, unites with the basioccipital (1), exoccipital (2) and supraoccipital (3), in almost equal proportions, and becomes directly perforated by the acoustic nerve (*ac*). Its chief foramen (*tr*), however, is, as usual, that which answers to the foramen ovale in the human alisphenoid, and which gives passage, as in fishes, to the great third division of the fifth, and to the branch which is homologous with the contribution by the fifth to the 'nervus lateralis' in many fishes, and at the same time with the nerve called 'chorda tympani' in anthropotomy.

In the frog I have given an external view of the alisphenoid (6) and the cartilaginous petrosal (16) in their undisturbed connections, in fig. 13, with the surrounding bones. The alisphenoid is here perforated, as in Man, by both a foramen ovale and foramen rotundum (*tr.*): it forms posteriorly the fore-part of the chamber for the cartilaginous petrosal, and usually coalesces with the mastoid (8), which overarches the petrosal: the back wall of the otocrane is contributed, as usual, by the exoccipital (2); the floor by the homologue of the coalesced basisphenoid and basioccipital. Had the outer part of the petrosal (16) been the seat of a partial ossification, a bone would have resulted corresponding precisely with Cuvier's 'rocher' in the cod and perch: but the immediate capsule of the labyrinth retains the same histological condition in the batrachia as it does in the carp and pike, and as in the salamandroid polypterus and lepidosteus: in the latter fish, at most, the only ossified part of the petrosal forms a small bony cup covering the posterior extremity of the outer semicircular canal*.

The attention of the justly celebrated ichthyotomist of Neuchatel appears to have been too exclusively occupied with the persistent embryonic condition of the 'petrosal' in these highly organized fishes, to gain that true and clear idea of the essential nature of the petrosal of which its partial ossification in the perch and cod is indicative. Adopting the opinion of Cuvier, in preference to that of Meckel and Hallmann, touching the special homology of the alisphenoid, M. Agassiz originally diverged into the opposite extreme of repudiating altogether the existence of a petrosal in the class of fishes. Thus, he says, "Il devrait suffire ce me semble de voir l'organe de l'ouïe présenter des modifications graduées dans toute la série des vertèbres, pour se convaincre que le *rocher* n'existe pas du tout chez les poissons, par plus que les osselets de la cavité du tympan. S'il y avait un *rocher* chez les poissons, ce devrait être un os qui entourerait le labyrinthe et les canaux semicirculaires; mais nous avons vu que ces parties de l'oreille interne se trouvent dans la cavité du crâne sans enveloppe osseuse particulière, et protégées seulement par les parois des os qui entourent le rocher, la ou il existe†."

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* This condition answers to that in the human embryo of about the fourth month, in which a light porous bony crust begins to be formed upon the cochlea and semicircular canals commencing with the outer and upper ones, the rest of the petrosal being cartilaginous.

† Recherches sur les Poissons Fossiles, tom. v. p. 66.

M. Agassiz is perfectly accurate in his character of the petrosal, according to its relative position, as completely investing the entire labyrinth (of which, by the way, the semicircular canals are an integrant part in all vertebrates and the largest part in fishes); but he takes a narrow view of its histological characters. The sclerotic is not less essentially a sclerotic in the shark, where it is cartilaginous, than it is in the cod, where it is osseous; neither is it less the eye-capsule and homotype of the petrosal in the mammal because it retains the earliest histological condition of the skeleton, viz. that of a fibrous membrane. And, in point of fact, in those fishes where the essential parts of the internal organ of hearing appear to be protected solely by the parietes of the bones, which, in the animals where the petrosal is ossified, or, as M. Agassiz expresses the fact, 'exists,' surround such petrosal, the vascular and nervous parts of the labyrinth are actually in such fishes more immediately enveloped by the petrosal in its membranous or cartilaginous states. What is peculiar to the petrosal in fishes is, that it is never entirely ossified; and, furthermore, that whenever it is partially ossified, the bony part is external and appears on the outside of the skull, instead of the inside as in crocodiles and birds.

In chelonians a larger proportion of the petrosal intervenes between the alisphenoid and exoccipital upon the inner wall of the cranial cavity than in crocodiles; but it is wholly cartilaginous. In birds, on the contrary, the whole petrosal capsule of the organ of hearing soon ossifies and becomes firmly anchylosed to the parts of the exoccipital, mastoid, alisphenoid and basisphenoid that form its primitive chamber or otocrane: owing, however, to the larger relative size of the ossified part of the proper capsule (petrosal proper) which penetrates the cranial cavity, none of the surrounding bones which contribute accessory protection, have received the name of 'rocher,' or *pars petrosa*. It was chiefly through not recognizing or appreciating the general nature or homology of the 'petrosal' that Cuvier failed to perceive its special homology in reptiles. Speaking of the skull of the crocodile, he says that the petrosal, or 'rocher,' is not less recognizable than the 'tympanic' and other so-called dismemberments of the temporal by its internal position, by its lodging a great part of the labyrinth, and by its contributing essentially to the formation of one of the fenestræ (*l. c.* p. 81). But the part in the crocodile which I regard as homologous with Cuvier's 'rocher' in the perch, is more completely internal in position than is Cuvier's so-called 'rocher' in the crocodile: it contributes a greater share to the formation of the 'fenestra vestibuli,' and it forms almost the whole of the 'fenestra cochleæ.' I have never found the alisphenoid (Cuvier's '*rocher*') in the crocodile, lodging a great proportion of the labyrinth*: the otocranial or petrosal process of the alisphenoid lodges a part only of the anterior semicircular canal, and no part at all of the other semicircular canals. The exoccipital is that tributary of the otocrane which lodges the major part of the labyrinth; it contains, for example, parts of two semicircular canals, and the rudimental cochlea: and, when the middle, usually distinct part of the petrosal is joined to it, the exoccipital may be said to form the whole 'fenestra cochleæ' and a greater part of the 'fenestra vestibuli.' We see, then, that the characters by which Cuvier deems his 'rocher' to be so easily recognizable, are more prominent in the exoccipital than in the alisphenoid: and the choice of the latter by Cuvier as the representative of the 'rocher,' seems chiefly to have been influenced by the more obvious and unmistakeable essential (neurapophysial) characters of the 'occipital latéral' (fig. 9, 2), whilst the accessory character which this bone derives from its lodging and becoming confluent with part of the true petrosal, was not allowed to prevail, as in the case of the alisphenoid, in the determination of its special homology.

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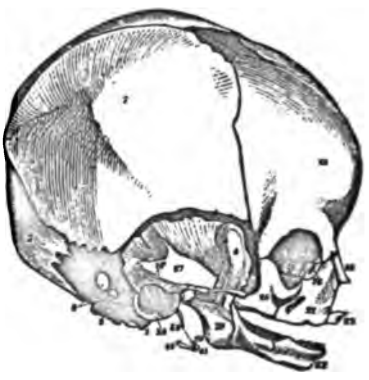
* "Il loge en grande partie le labyrinthe," *l. c.* p. 81.

The supraoccipital, by virtue of its internal position and lodgment of part of the labyrinth, has equal claims to the name of 'rocher,' according to the Cuvierian characters of that bone, and Geoffroy St. Hilaire did not make a less arbitrary choice in singling out this element as 'le seul rupéal*,' than Cuvier did in choosing the alisphenoid, or, as any other anatomist would do in preferring any other element of a cranial vertebra in the crocodile to represent the ossified ear-capsule of the fish or mammal, because portions of that ossified capsule are protected by, or have coalesced with, such vertebral elements. Had Cuvier looked beyond the special homology of the bones of the head of the crocodile, and permitted himself to appreciate their higher and more general relations, he could scarcely have failed to perceive the correspondence of his so-called 'rocher' in batrachians, ophidians, chelonians and saurians, to the bone which he so well recognizes as 'the great wing of the sphenoid' in the perch and cod-fish.

The Mastoid.—In the human embryo of the fifth month a centre of ossification is established on the outer surface of the mass of cartilage occupying the interspace between the basioccipital (fig. 11, 1) and exoccipital (2) below, the tympanic (28) and squamosal (27) in front, the supraoccipital (3) behind, and the parietal (7) above: this mass of cartilage incloses the membranous labyrinth, about which a light osseous crust has begun to be formed; and, from the centre (8) established near the outer border of the posterior semicircular canal, ossification radiates to complete that part of the cranial parietes, which, in the adult skull, is impressed on its inner surface by the great venous channel called 'fossa sigmoidea,' and developes from its outer surface the 'processus mastoideus.' The primitive independence of the base of this process, which Kerkringius so clearly and accurately delineates in his *tab.* xxxv. *fig.* iii. as the posterior of his 'tria petrosi ossis distincta ossicula†,' is a fact of much more significance than its brief and transitory manifestation would lead the anthropotomist to divine. The coalescence of the primitively distinct mastoid with the ossifying capsule of the labyrinth is very speedy, being usually complete before the fœtus has passed its fifth month, and a composite 'petro-mastoid' bone is thus formed, which, retaining its individuality in monotremes, marsupials, ruminants and many rodents, proceeds to coalesce with the additional elements of the 'temporal' bone in man, and with other surrounding cranial bones in birds. In the cold-blooded vertebrata, the mastoid retains, with a few exceptions, its primary embryonic distinctness, as an independent element of the skull. In tracing the modifications of this element downwards from man, we find the external process from which its anthropotomical name originated,

Fig. 11.



Skull of the human embryo; fifth month. Natural size.

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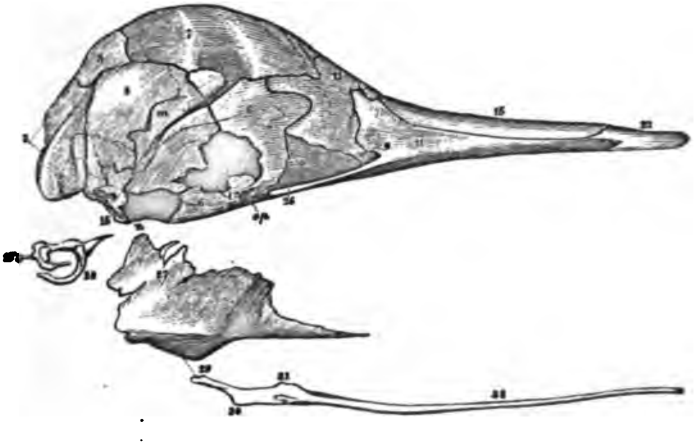
[*] Annales des Sciences Naturelles, tom. iii. 1824, p. 271, pl. 16.
[†] Spicilegium Anatomicum, 4to. 1670, Osteogenia Fœtuum, p. 260.

inconstant, its functions being transferred in many mammals to another process, sometimes udder-shaped, sometimes of great length (fig. 24, 4), but which is developed from the exoccipital, and is represented in the human skull by the 'eminentia aspera,' &c. of Soemmerring (TABLE I. 4), and by the "scabrous ridge extended from the middle of the condyle towards the root of the mastoid process" of Munro (*op. cit.* p. 72): but sometimes also here developed, as a rare anomaly, on one or both sides, into a process like a second but smaller posterior mastoid *. The more constant and essential characters of the mastoid are its contribution to the walls of the acoustic chamber, carried to anchylosis with the petrosal in birds and mammals, and its sutural connection in the latter with the exoccipital, parietal, and squamosal (the squamo-mastoid suture becoming obliterated in many species, *e. g.* the hog, fig. 24, 8, 27): it is also grooved, notched or perforated by a greater or less proportion of the lateral venous sinus, whether this is continued to the 'foramen jugulare,' as in man, or sends a large division to escape by the 'meatus temporalis' which forms the large orifice between the mastoid and squamosal above the meatus auditorius in the horse and ruminants, and which directly perforates the mastoid in the echidna (fig. 12, m).

Fig. 12.



Partially disarticulated cranium of the *Echidna setosa*. Natural size.

It is important to keep these essential characters steadily in view, and to avoid giving undue importance to the apophysial character of the mastoid, which has led to so common a transference of its name, in the great osteological works of Cuvier and De Blainville, to a quite distinct element (paroccipital) of the cranial walls †. It is necessary, also, to be prepared for that change of the connections of the mastoid, which results from the gradual withdrawal, in the mammalian class, of the squamosal from the proper cranial walls. With much inconstancy of relative size in the mastoid, of which the dugong and the walrus offer two extremes, we discern upon the whole a progressive increase in descending through the mammalian class: in the walrus, for example, the mastoid, or petromastoid, forms as large a proportion of the outer lateral walls of the cranium as does the squamosal; and, in the sheep, the removal of the squamosal exposes the connection of the petromastoid with the alisphenoid,—a return to a relation common in the oviparous vertebrata: it is shown from the inner side of the cranium in the sheep, in fig. 7, 16 and 6. The mastoid of the echidna (fig. 12, 8) presents a most interesting and instructive combination of both the modification of expansion and of that of direct union with the alisphenoid (6), which is here effected by the mastoid plate independently of the petrosal (16). In fig. 12 these characters are well exposed by the removal of the squamosal 27, and tympanic 28, which retain their primitive independence throughout life in the echidna. If now we compare the bone 8 and 16 with the cartilaginous and osseous mass 8 and 16 in the skull of the human embryo (fig. 11), and allow for the change produced in the position of the alisphenoid (6) by the gradual withdrawal of the squamosal (27), traceable in the intervening forms of mammalia, the special homology of the petromastoids at the two extremes of the mammalian class will be obvious and unmistakeable. The bone 8 and 16 in the echidna, fig. 12, is connected below and behind with the basioccipital and exoccipital (2), behind and above with the supraoccipital (3) and parietal (7), in front with the tympanic, the squamosal, and also, as a consequence of the modified position of the latter and of its own increased development, with the alisphenoid (6). All the connections, save that with the alisphenoid, are identical with those of 8 and 16 in the human embryo; and the supervening alisphenoidal connection in the echidna affords an additional light to the determination of the bone in the lower vertebrata, since it is a consequence of the progressive advance to a lower (oviparous) type, in the descent through the mammalian scale. In regard to the essential functions of the petromastoid, we find the petrosal portion inclosing the membranous labyrinth, and the mastoidal portion giving exit to the blood from the great lateral venous sinus and supporting the tympanic*. It will be unnecessary to dwell further on the broad and obvious characters by which the homology of the bone 8 and 16 in the echidna is established with the equally independent petromastoid in the sheep and walrus, and with the petromastoid portion of the human 'temporal bone.'

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* The continuators of Cuvier make mention of an example of this kind and propose the name of 'paramastoid' for the process (Leçons d'Anat. Comp. ii. (1837) p. 312). I have observed it in the skull of a New Zealander and in that of an Irishman, preserved in the Museum of Anatomy in Richmond Street, Dublin. Believing it to be the homologue of the 'paroccipital' (4), which is developed independently in chelonia and most fishes, I retain that name for it: it must not be confounded with that angle of the occipital which projects into the 'foramen jugulare' in the human skull, and which has received the name of 'processus jugularis,' in some systems of anthropotomy.

† How essential a correct view of special homology becomes to the appreciation of the

The continuators of the 'Leçons d'Anatomie Comparée,' influenced by the large proportional size of the petromastoid in the echidna and the share which it consequently takes in the formation of the cranial parietes, supposed it to be the squamosal:—"le véritable temporal, qui n'aurait pour toute apophyse zygomatique qu'un très petit tubercule près de la facette glénoïde,"

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higher law of general homology may be learnt from the application by Cuvier of his idea of the mammalian mastoid to the refutation of the vertebral theory of the skull. "On a aussi trouvé quelque rapport entre l'apophyse mastoïde qui, dans la plupart des animaux, appartient à l'occipital, et l'apophyse transverse de l'atlas et des autres vertèbres; sur quoi il faut remarquer que ces rapports sont moindres dans l'homme à certains égards que dans les quadrupèdes, puisque l'atlas n'y a ordinairement qu'une echancrure pour le passage de l'artère, et que l'apophyse mastoïde y appartient entière au rocher."—Resumé sur le question—'Le crâne est-il une vertèbre ou un composé de trois ou quatre vertèbres?' Leçons d'Anatomie Comparée, t. ii. (1837) p. 711.

* In the article 'Monotremata,' Cyclopædia of Anatomy and Physiology, 1841, I described the petromastoid as the petrous bone, misled by the absence of the external character of the process.

op. cit. t. ii. (1837) p. 377. This tubercle is the rudiment of the mastoid process, which is so largely developed in birds, and which, in the echidna, overhangs the tympanic cavity. There is no glenoid articular surface upon the bone 8 and 16. We find, on the other hand, the squamosal under its proper mammalian form and connections, with a long and slender zygomatic process, and performing the function, peculiar to the class Mammalia, of supporting the mandible by the true glenoid articular surface in the echidna (fig. 12, 27).

Dr. Köstlin, whose painstaking and minutely accurate description of the osteology of the vertebrate skull renders his conclusions as to their homologies worthy of respectful consideration, concurs with me in regard to the squamosal (27) of the monotremes, but regards the bone 8–16 in the echidna as a dismemberment of the alisphenoid. In no mammal, however, do we find the alisphenoid concerned in immediately protecting the semicircular canals—this is the function of the petrosal: in neither mammal nor bird does the alisphenoid extend its connections so far back as to the basi-ex- and supra-occipitals. In the echidna, as in every other mammal and bird, the alisphenoid (6) exists, exclusively exercising its essential function of transmitting the third division of the fifth pair by the large vacuity (*tr*) and with its normal connections modified only, as in the sheep and some other inferior mammalia, through the recession of the squamosal, by joining the mastoid, in addition to those which it unites with in man. I confess that I can perceive no other gain to anatomy by Dr. Köstlin's new determination of 8 and 16 in the echidna as 'hintere Abtheilung des Schläfenflügels' or 'hintern Schläfenflügel*' (posterior alisphenoid), than an additional phrase to the synonyms of the mastoid.

The discussion of the homologies of this bone under its modifications in the mammalia, and especially in the monotremata, will not be deemed superfluous or too detailed, when it is remembered how valuable a key the cranial organization of the implacental monotremes with their bird-like heads becomes to the comprehension of the modifications of the cranial structure in birds themselves. If we pass from the comparison of the echidna's skull, as represented in fig. 12, to that of the ostrich (fig. 8), we shall find there a bone (8) articulated in front to the alisphenoid (6), behind to the exoccipital (2), below to the basi-occipital and basi-sphenoid, above to the parietal 7, and coalescing by its inner surface with the petrosal. The sole modification of note in regard to connective characters, as compared with the mammalian petromastoid, is the loss of the connection with the squamosal, for which we have been progressively prepared by the conditions of that bone in rodents, ruminants and monotremes. In the bird this least constant element of the cranial walls (fig. 21, 27) has undergone a further degradation, is now dismissed entirely from any share in the formation of even the outer surface of the cranial parietes, and is reduced to its mere zygomatic form and function, serving exclusively to connect the jugal (fig. 21, 26) with the tympanic (28); which function it performs in the echidna and in man, besides other superadded offices arising out of its peculiarly mammalian expansion into a scale-like lamina, or as compensatory of the reduction of the tympanic bone. Dr. Hallmann, however, in his elaborate monograph on the temporal bone, considers the bone 8 (fig. 8) to be the squamous or zygomatic element, and cites the following characters of the bone, in the young cassowary†, as establishing its homology with the squamosal:—"its junction above with the parietal, in front with the alisphenoid and post-frontal and behind with the occipital; also its formation of the upper border of the meatus auditorius externus, and its contribution of the articular surface for the tympanic bone," which surface he regards as homologous with the glenoid cavity of the squamosal for the lower jaw in mammals.

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* *Op. cit.* pp. 29, 126.

† Die vergleichende Osteologie des Schläfenbeins, p. 8. pl. 1. fig. 5.

Cuvier, whose homology of no. 8 he thus adopts, describes it in the bird as being on the outer side of the parietal, advancing also to beneath the frontals, occupying the region of the temporal fossa and giving origin to the temporal muscle, and as forming the superior border of the tympanic cavity. "The temporal fossa," adds Cuvier, "is in great part excavated in the temporal bone, and is bounded behind by a special process which might be regarded as the analogue of the zygomatic did it not remain far removed from the jugal bone*." The annotators add, "that there are some species of bird in which, nevertheless, such zygomatic process does approach very close to the jugal†."

First, then, with regard to the character which appears to have most weighed with Cuvier, from his twice citing it in the above brief definition of no. 8,—the marks of the origin of the temporal muscle. To conclude that the bone impressed by the so-called 'temporal fossa' in the skull of the bird, is therefore the temporal bone, because such fossa impresses a bone called 'temporal' in the mammal, is an example of that fallacy which logicians call arguing in a circle. The two propositions by no means reciprocally prove each other. Suppose, for example, that the bone no. 8 in the bird had been determined, by way of ascensive comparison from the fish (fig. 5) and crocodile (fig. 16), to be the homologue of the bone no. 8 in those animals, which we will assume to have been rightly called 'mastoid' by Cuvier, and that he had arrived at the determination of no. 8 in the bird by this surer method, than by the descent from placental mammals; and supposing that, having thus recognized no. 8 as the mastoid, the fossa and muscle with which it is impressed in the bird had been called 'mastoidal' instead of 'temporal'; then, ascending to the mammalian cranium, Cuvier might with equal reason have said that the bone 27, figs. 11 and 22, was the 'mastoid,' because it occupied the region of the mastoidal fossa and gave origin to the mastoidal muscle. The origins of muscles are not, however, sufficiently constant to be included amongst the characters of connection or function determinative of special homologies. The transference of the 'sterno-mastoideus' from the true mastoid process (Man, carnivores and rodents) to the angle of the mandible (horse), and to both this part and the second cervical vertebra (ruminants), shows that the attachments of a muscle must be determined after the recognition of the bone, and not the homology of the bone by muscular attachments. With the very case in question the uncertainty of the character is illustrated: in the skull of the ostrich, for example (fig. 8), the temporal fossa is chiefly formed by the conjoined portions of the parietal (7) and alisphenoid (6), which intervene between the mastoid (8) and the postfrontal, the mastoid forming not more of the posterior part of the fossa than the postfrontal does of the anterior part. Dr. Hallmann probably appreciated the unsoundness of the argument from the muscular impression, since he does not cite it; he repeats, however, the character adduced by Cuvier, from the relation of no. 8 to the tympanic cavity, or as Hallmann expresses it, the meatus auditorius (äussern Gehör öffnung), the value of which therefore I next proceed to consider.

In the skull of the ostrich, with the tympanic bone and ear-drum in place, the upper border of the meatus, as defined by the periphery of the membrana tympani, is formed, not by no. 8, but by the tympanic anteriorly, and by the paroccipital process (4) posteriorly. When the tympanic bone and membrane are removed, then the descending process of no. 8 overarches the upper and forepart of the tympanic cavity so exposed. So much for the facts of the argument*.

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* Leçons d'Anat. Comp. ii. (1837), p. 580.

† Ib. p. 581.

We may next ask, Is the formation of the upper boundary of the meatus externus an essential character of the squamosal in mammals; or is it not rather a secondary consequence of the expansion and application of that bone to the side of the cranium in this particular class? If we were desirous of obtaining a homological character by comparison of the contour of the meatus externus or the tympanic cavity in mammals and birds, ought we not rather to select the lowest and most ornithoid of mammals, as best calculated to throw light upon the real nature of the modifications of this part of the skull in the respective classes? In the echidna, then, we find that the squamosal does not form the whole of the superior border of the shallow tympanic cavity, but that the mastoid forms the posterior half of that border, and sends a short obtuse process downwards (at 16, fig. 12), which overhangs the cavity and gives attachment to the tympanic (28). Behind the mastoid is the exoccipital. Now in birds the antero-posterior extent of the cranium between the exoccipital and postfrontal bones is much shortened as compared with mammals, and this modification I interpret as the result, in a great degree, of the entire removal of the squamosal from the cranial parietes. Of the homology of no. 4 as a part of the exoccipital there has been no question, although its development, and the share it takes in the lateral parietes of the head, is increased, as compared with most mammals, rather than diminished. The exoccipital constantly unites anteriorly with the mastoid in mammals, from man down to the echidna; but the extension of the squamosal backwards to articulate with the exoccipital is far from being a constant character in mammals. We ought on that ground therefore to conclude that the bone 8, which articulates with the fore-part of the exoccipital in the bird, is the 'mastoid,' rather than that it is the 'squamosal.' It overhangs the tympanic cavity by a longer or shorter process; but being more advanced in position, partly by the development of the exoccipital behind, and the non-interposition of a squamosal between it and the alisphenoid in front, it overarches the middle of the upper instead of the posterior part of the upper border of the tympanic cavity in the bird; but it is still in great part posterior to the tympanic pedicle, a relative position which is foreign to the squamosal. The process of no. 8 resembles the mastoid process in mammalia, inasmuch as it terminates freely in most birds; and in those, the parrot for example (pl. 1, fig. 1, 8), in which it joins another process to form a zygoma or bridge over the temporal fossa, that process answers to the postfrontal, the very bone which the mastoid similarly joins in the crocodile, and does not answer to the malar bone, which the squamosal joins in both mammals and crocodiles.

The mastoid always coalesces with the petrosal, rarely with the squamosal, in the mammalia; such coalescence is therefore a more constant character of the mastoid than of the squamosal, and the argument becomes cumulative in favour of the mastoid or petromastoid character of no. 8 in the bird. When we remove the squamosal in the sheep we bring away the mandible which articulates with it, but we leave the distinct and independent tympanic closely articulated to the petromastoid. Precisely the same thing happens in the rodentia, in the marsupialia, and especially in the echidna, in which the tympanic has the slightest connection with the squamosal. The articulation of the tympanic therefore with the petromastoid is a more constant character than its articulation with the squamosal; therefore the articulation of the unquestioned tympanic bone in birds with the bone no. 8 is a stronger proof of no. 8 being the petromastoid than of its being the squamosal: and for the same reasons that the articulation of no. 8 with the exoccipital, and its coalescence with the petrosal, are more essential characters of the petromastoid than they are of the squamosal, so I regard the articular surface furnished by no. 8 to the tympanic bone to be homologous with the articular surface of the petromastoid for the tympanic in the ruminants, rodents and other mammals, and am compelled to dissent from Dr. Hallmann's idea of its answering to the articular surface furnished by the squamosal to the mandible in mammals. In the ostrich a part of the articular cavity for the tympanic is excavated in the exoccipital, and would afford as good an argument to prove that bone to be the squamosal as the one which Dr. Hallmann has deduced from the same character in favour of the petromastoid in the bird being the squamosal. Dr. Hallmann cites the junction of no. 8 (his *t*, taf. i. fig. 5, *op. cit.*) with the postfrontal in a young cassowary as evidence of its squamous character. I have not met with this union in the young ostrich nor in the young emeu, in which latter bird there is a distinct postfrontal: the anterior inferior angle of the parietal descends and meets the alisphenoid in both these *Struthionidæ*, at the part where the post-frontal is marked (at *f''*) in Dr. Hallmann's figure above cited. The extremity of the mastoid process does, however, arch over the temporal fossa to join the postfrontal process in certain birds, as above mentioned; but this junction, when we ascend in our pursuit of the homologies of the elements of the composite temporal bone of mammals, as it is safest to do, from fishes to reptiles, and from these to birds, forms a repetition of a very characteristic feature of the mastoid in the cold-blooded classes, and one that is quite intelligible when we rise to the appreciation of the higher relations of both mastoid and post-frontal as parapophyses of their respective vertebræ.

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* The same formation of the upper boundary of the meatus externus is shown by Geoffroy in the young fowl.—Annales du Muséum, x. pl. 27. fig. 2. V. Q.

In every mammal the squamosal is applied to the cranial parietes, and attached by a peculiar suture called squamous; the outer surface of the bone exceeding the inner surface. In no bird is the mastoid so united to the surrounding bones, but joins them by harmoniæ vertical to the surface, as the other true cranial bones are joined before they coalesce; and the outer very little, if at all, surpasses the inner surface, to which the petrosal is confluent. The petromastoid of the mammal resembles that of the bird in this respect.

There is no difficulty in the ascensive survey in appreciating the special homology of no. 8 in the bird (fig. 23) with no. 8 in the crocodile (fig. 22) and in the fish (fig. 5); and Dr. Hallmann, retaining a firmer and more consistent view of their common characters than Cuvier, enunciates clearly this homology: but having persuaded himself that the 'mastoid' of the bird was its 'squamosal,' he concludes that the bone which Cuvier had called mastoid in the crocodile and fish must also be their squamosal. I believe Cuvier to have rightly determined the bone (no. 8) in the cold-blooded classes to be the mastoid; but he is not consistent with himself when he adopts a different conclusion with regard to no. 8 in the bird. The greater development of the bird's brain, as compared with the crocodile's, requires a greater expansion of the cranial part of the mastoid, just as the still greater development of the brain in mammals calls forth a peculiar expansion and application of the cranial end of the squamosal, involving a transference of the mandibular joint to that expanded end.

Cuvier, in descending from mammals to the consideration of the homologies of no. 8 in the bird, passed too abruptly to the comparison, lacking the instructive link furnished by the monotremes. It might have sufficed for the present report to have demonstrated the homology of no. 8 in the bird, ascensively, with Cuvier's well-determined mastoids in fishes and reptiles;

but since both Cuvier and Dr. Hallmann have elucidated their views of its homology by characters drawn from the mammalian class, I have endeavoured, and I trust satisfactorily, to meet their objections and to determine the true homology of the bone by other arguments drawn from modifications of the petromastoid in the same class.

Pursuing therefore the comparison descensively, I proceed in the next place to consider the characters of the mastoid in the crocodile (figs. 19 and 22, *8*). Cuvier premises his determination of the bone in that reptile by citing the following as its characters in the mammalia:—"La partie mastoïdienne qui recouvre le rocher en arrière de l'écailleuse et de la caisse, mais qui se soude de si bonne heure à ce rocher que l'on paroient à peine à la reconnaître comme distincte dans les plus jeunes fétus où elle est quelquefois double[*]." The squamosal he defines as a bone "qui devient de plus en plus étrangère au crâne à mesure qu'on descend dans l'échelle des quadrupèdes, en sorte que dans les ruminans elle est plutôt collée dessus qu'elle n'entre dans la composition de ses parois[†]." If we pause to apply these characters to the determination of nos. *8* and *27* respectively in the bird, before proceeding to the crocodile, we shall see how far they sustain the conclusions I have arrived at, in opposition to the views of Cuvier and his followers, in reference to the true homologue of the mammalian squamosal in birds. With regard to the mastoid in the crocodile, Cuvier says, "Le mastoïdien des crocodiles proprement dits et des gavials a cela de particulier, qu'il s'avance latéralement jusqu'à s'unir au frontal postérieur, et à entourer avec lui et le pariétal le trou de la face supérieure du crâne qui communique avec la fosse temporale; dans quelques caïmans il s'unit même à ces trois os pour couvrir entièrement cette fosse en dessus, et dans les tortues de mer, non-seulement ils font la même chose, le temporale et le jugal venant aussi à s'unir au mastoïdien et au frontal postérieure, ils couvrent la fosse temporale, même par dehors."[‡]

Doubtless the German anatomists who dissent from Cuvier's determination of the bone *8* in the crocodile (fig. 22) have been influenced in some degree by the little conformity between the character above assigned to the mastoid in that reptile and the character Cuvier had previously assigned to the mastoid in mammalia. The confluence of the mastoid with the petrosal, for example, is a modification peculiar to the warm-blooded vertebrates, whilst the relative position of the mastoid, above and external to the petrosal, above and behind the tympanic, and behind the squamosal, when this bone is present, is a constant character in all vertebrates; to which must be added, that in most mammals and all other vertebrates the mastoid affords an articular surface for the tympanic bone, and developes an outstanding (mastoid) process for the attachment of strong muscles moving the head upon the trunk. With regard to the relative position of the mastoid process to the cranial walls, its origin ascends as the expansion and elevation of the parietal diminishes with the decreasing size of the cerebrum: in mammals, the process, when present, extends from the lower border of the postero-lateral wall of the cranium: in birds it projects from near the middle of that wall, and nearer the upper surface in the flat-headed *Dinornis*: in the crocodile it has ascended to a level with the upper surface of the cranium, and forms the posterior angle of that surface. The paroccipital presents a similar progressive ascent, but later in the series traced descensively; it does not gain the level of the mastoid until we arrive at the class of fishes.

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[*] *Op. cit.* t. v. pt. ii. p. 81.

[†] *Ib.* p. 81. Oken notices the completion of the cranial cavity, independently of the squamosal, in the sheep; in his "Programm", &c. 4to. 1807, p. 8.

[‡] *Ib.* p. 84.

The mastoid, thus determined in the crocodile, is recognized with ease and certainty in chelonia, lacertia and ophidia. It is a distinct bone in all these reptiles, and preserves with singular constancy its normal relative position anterior to the exoccipital, superior to and supporting the tympanic, and anterior to the squamosal when this is present. In lizards the mastoid is much reduced in size: in serpents it attains a considerable length. In the python and most serpents it forms no part of the proper wall of the cranium, but overlaps the contiguous parts of the parietal, alisphenoid, supra-occipital, and exoccipital, projecting backwards beyond the latter. It is large in the serpentiform batrachia, but presents in *Cæcilia* (Cuvier, Règne Animal, 1817, pl. 6. figs. 1 & 2, *g*) its normal connections with the occipital (*f*), parietal (*e*), tympanic (*h*), and also with the post-frontal, which has coalesced or is connate with the frontal (at *d*, l. c.). Cuvier does not admit of this confluence in the cæcilia; and although he assigns the character 'point des frontaux postérieures' to the typical batrachia*, gives the name 'posterior frontal' with a note of doubt, indeed, to *g*, and assigns to the bone *h*, which suspends the mandible, the name of "mastoïdiens et caisses réunis†." There is no actual necessity for assuming so rare a confluence to characterize the cæcilia. The mastoid exists with all its normal connections, and beautifully manifests by its independence and large size the affinity of the cæcilia to the true ophidia. In the typical batrachia, where the cranium is remarkably characterized by instances of confluence which seem borrowed from the warm-blooded classes, the mastoid sometimes loses its independence, and appears as an exogenous process from the external and posterior part of the parietal, retaining however its normal office of suspending the tympanic: but in a skull of the *Rana boans* now before me, the suture between the mastoid (fig. 13, 8) and parietal (7) is not obliterated, and it further articulates with the exoccipital (2) behind and the alisphenoid (6) in front. Cuvier, in his description of the tympanic of the *Rana esculenta*‡, says, that its upper branch articulates with the 'rocher.' In *Rana boans* that branch articulates exclusively with the truncated extremity of the broad outstanding mastoid, which mastoid overhangs, as in all fishes, the petrosal, which is chiefly cartilaginous in the *Rana boans* (*ib.* 16). In *Rana esculenta* the mastoid (Dugès, Recherches sur les Batrachiens, fig. 1, 12) appears to have coalesced with the alisphenoid (*ib.* figs. 2, 6 & 7, 12); and the compound bone has received the name of 'rocher' from Cuvier and that of 'rupéo-ptéreal' from Dugès. The foramen ovale however marks the alisphenoidal part (a distinct bone in my *Rana boans*), and the suspension of the tympanic marks the mastoid, which, with its other connections, overhangs also in *Rana viridis* that mass of cartilage§ which immediately invests the membranous labyrinth and forms the 'fenestra ovalis' against which the plate of the columelliform stapes is applied.

Prof. J. Muller has well recognized the homologue of this sense capsule in the *Cæcilia hypocyanea*, in which he describes it as "petrosum cum operculo fenestræ ovalis‖." It is situated further back than in *Rana*, and appears posterior to the tympanic (*i*) and the large suspending mastoid (*h*), to which Muller gives the name of 'temporale.' In the singularly modified cranium of the *Tythlops* the mastoid articulates above with the parietal and supraoccipital, behind with the exoccipital, coalesces in front with the alisphenoid, as in some batrachia, and affords the usual articulation below to the tympanic.

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[*] Ossem. Fossiles, v. pt. i. p. 386.

[†] Règne Animal, ed. 1817, t. iv. p. 102.

[‡] Ossem. Fossiles v. pt. ii. p. 390.

[§] The precocious development of this capsule in the larva of the frog is well shown by Reichert, 'Entwickelungsgeschichte des Kopfes,' 4to, pl. i. figs. 13—15, *s*: it resembles that in the myxinoids and lampreys.

[‖] Beiträge zur Anatomie der Amphibien; Tiedemann's Zeitschrift für Physiologie, Bd. iv. 1831, p. 218, pl. 18. fig. v. *h*.

How necessary it is to retain a clear and consistent appreciation of these evidences of the homology of the mastoid is shown by the second synonym, 'os petrosum,' which it has received from the justly-celebrated author of this instructive memoir (pl. 20. figg. 10, 12, 13, 14, *p*). The actual capsule of the membranous labyrinth is covered by the mastoid and exoccipital, and remains wholly cartilaginous, as in other ophidia; and as it likewise does in *Rhinophis*, where its name 'petrosum' is in like manner transferred by Prof. Muller to the coalesced mastoid and alisphenoid. In *Cheirotes* the course of confluence proceeds to obliterate not only the suture between the mastoid and alisphenoid, but that between the mastoid and parietal; as also of those between the frontal, parietal and supra-occipital; the whole cranium presenting almost the extent of coalescence which characterizes the hot-blooded bird. Only the immediate covering of the membranous labyrinth remains cartilaginous.

The sides of the superior surface of the cranium of bony fishes usually extend outwards as a strong irregular ridge, from which three processes more particularly project, which are supported by three distinct bones, suturally united, and each impressed with an articular glenoid cavity. And here I cannot avoid remarking how beautifully the principle of vegetative repetition[*] is exemplified in the lowest class of the Vertebrata, where consequently the relations of serial homology of the parapophyses in question are unmistakeable. The posterior process or bone which sustains (in part) tha scapular arch is the paroccipital (fig. 5, 4); the anterior one, which sustains in part the tympano-mandibular arch, is the post-frontal (*ib.* 12); and the intermediate and usually most prominent bone (*ib.* 8), which sustains in part the epitympanic (38*a*), and through that the hyoid arch, is the homologue of the bone whose essential characters have been discussed under the name of 'mastoid.' The paroccipital having now risen to a level with the mastoid, this forms the second strong transverse process at each side of the cranium. The process is developed from the outer margin of the mastoid; the inner side of the bone is expanded, and enters slightly into the formation of the walls of the cranial or rather the otocranial cavity, its inner, usually cartilaginous surface lodging the fibro-cartilaginous continuation of the petrosal which immediately covers the external semicircular canal. It is wedged into the interspace of the ex- and par-occipitals, the petrosal, the alisphenoid, the parietal and post-frontal bones. The projecting process lodges above the chief mucous canal of the head, and below affords attachment to the epitympanic or upper piece of the bony pedicle from which the mandibular, hyoid, and opercular bones are suspended: its extremity gives attachment to the strong tendon of the dorso-lateral muscles of the trunk.

It might have been supposed that this contribution to the walls of the cranial cavity, this articulation to the occipital and tympanic bones, all of which are constant characters of the mastoid in mammals, and but occasional ones in the squamosal—not to speak of the apophysial form and functions of the bone in question in the skull of fishes—would have made the balance incline to the choice of the 'mastoid' rather than of the 'squamosal' elements of the human temporal in the judgement of every unbiassed investigator of its homologies. The German anatomists, however, in falling with Cuvier into the mistake respecting the homology of the 'mastoid' (no. 8) in birds, with the squamosal in mammals, adhere more consistently to their error and continue to apply the name 'squamosal' or its equivalents to the homologous bone in reptiles (fig. 22, 8) and fishes (fig. 5, 8).

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[*] This principle or law is explained in the first volume of my Hunterian Lectures 'On the Invertebrata,' 8vo. 1843, in which classes of animals it is most strikingly and fully exemplified.

The high repute which M. Agassiz has so justly earned in ichthyotomy renders the accession of his name in support of Drs. Hallmann, Reichert, and Köstlin's determination of the bone in question, one to which those able homologists and their followers will naturally attach great weight, and which indeed has caused me to pause and retrace more than once, and with the utmost pains and care, every step in the series of comparisons which have finally brought conviction of the accuracy of the Cuvierian determination of no. 8 in fishes.

I am not aware that any anatomist has replied to the objections to the Cuvierian view propounded by M. Agassiz. Drs. Hallmann and Köstlin, who have published the most elaborate monographs on the temporal and other bones of the skull since the time of Cuvier, concur entirely with the learned Swiss naturalist. Dr. Reichert, in giving the name of 'squama temporalis' to no. 8, and that of 'processus temporalis posterior' to its process, transfers the name 'processus mastoideus' to the paroccipital (no. 4, fig. 5)*. It becomes then necessary to consider the arguments of M. Agassiz in favour of the homology of no. 8. in fishes with the squamosal no. 27 in mammals. In the valuable monograph on the osteology of the pike (*Esox*) in the 15th 'Livraison' of the 'Recherches sur les Poissons Fossiles,' the author says (p. 66), "Un os de la tête placé entre le frontal postérieur, le frontal principal, le pariétal, la grand aile sphénoïdale et l'occipital latéral, ne saurait jamais être envisagé comme correspondant à l'apophyse mastoïdienne du temporal. D'après ses liaisons, je crois donc qu'il faut envisager le *mastoïdien* de Cuvier comme l'analogue de l'*écaille du temporal* ou comme le *temporal* proprement dit. C'était déjà l'opinion de Spix, qui est tombé juste sur ce point." To this I reply that, in regard to the connections of the mastoid, those with the parietal, alisphenoid and exoccipital, are more constant than that with the frontal, which is interrupted in mammalia by the interposition of the expanded squamosal, peculiar to that class; but the mastoid retains its piscine connection with the postfrontal in many reptiles and some birds. On the other hand, the union of the squamosal with the frontal is by no means a constant character in mammalia: it is rarely found in the orang, still more rarely in man, never in the cetacea and monotremes, nor in certain ruminants, nor in the myrmecophaga, &c. The connection of the mastoid with the frontal is more common than is the connection of the squamosal with the exoccipital. It is a bold leap to take from the mammal to the fish in the determination of a variable bone like the squamosal: nevertheless, I would request the unbiassed reader to glance at fig. 12, whilst he reads M. Agassiz's *précis* of the character of the squamosal above cited, and see how far no. 8 deviates from it, save in regard to the frontal connection. Spix, who appears not to have traced the beautiful gradation of the mastoid in the mammalia, and who was unacquainted with the decisive step to its normal condition in the oviparous vertebrates made by the monotremes,—and who was influenced, therefore, by seeing that bone in higher mammals pushed back from any connection with the alisphenoid and postfrontal by the interposed squamosal, which usurps these connections and combines them with others, as with the parietal and tympanic, which the mastoid (no. 8) presents in fishes,—not unreasonably concluded that no. 8 represented the squamosal in that class; and it is probable that M. Agassiz, who received his anatomical rudiments at Munich, and was early engaged in describing the fishes collected in Brazil by the author of the 'Cephalogenesis,' might have derived a bias in favour of this view which prevented his assigning their due value to the connection of no. 8 in fishes with the paroccipital, and its contribution to the otocranial cavity.

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* *Op. cit.* tab. iii. figs. 9 and 13, *p*, *q*.

In urging a reconsideration of the value and significancy of these characters, I may repeat that in mammals the mastoid constantly presents them, whilst the squamosal very rarely has the first, and not often the second character. It must also be remembered that the squamosal loses its connection with the frontal and progressively decreases in the mammalian class to less than the dimensions of the mastoid itself, as *e. g.* in echidna (fig. 12), whilst in this monotreme the mastoid, 8, besides its connections with the parietal and exoccipital, extends forwards to articulate with the alisphenoid, 6. If ossification were restricted in mammals to no. 8, fig. 11, in reference to 16, which remained cartilaginous, then no. 8 would have the same relation to the otocrane, or in other words, would contribute the same protection to the acoustic labyrinth, which no. 8, fig. 5, performs in fishes; the external semicircular canal at least would be protected by the mastoid in both: only in mammalia the mastoid would also extend over the posterior canal. The petrosal loses no part of its essential character as the capsule or outer tunic of the labyrinth by becoming ossified, nor is it less recognisable in fishes within the mastoid, by remaining membranous or cartilaginous, than is the sclerotic capsule of the eye in its chamber or orbit; which capsule, in like manner, presents all the corresponding histological modifications in one or other part of the vertebrate series. The mask which has concealed the true features of resemblance of the human mastoid to that of fishes, is simply the petrosal ossified and cemented to it. But the squamosal presents no such relations to the bony capsule of the semicircular canals in any mammal. Even the connection of the squamosal with the tympanic bone is, as we have seen, far less constant and intimate in mammals than the connection of the mastoid with the tympanic*.

In the anatomical description of the existing ganoid fishes which M. Agassiz has unfortunately called 'Sauroid†,' the bone no. 8 is described as taking part, by its large size, in the formation of both the internal and external surfaces of the cranial* box, which size depends essentially on the degree of development of the frontals, parietals and occipitals: it is further urged that the suborbitals ('apophyse jugale') are likewise attached to it; that the preopercular ('apophyse styloïde') diverges, and is directed or abuts against it; that, finally, the bone in question (no. 8, fig. 5) is, with the exception of the petrosal, the sole part of the temporal bone which takes a direct part in the formation of the cranial box. "D'après ces considérations," M. Agassiz proceeds, "il est impossible de prendre l'os No. 12 [no. 8, in fig. 5], que Cuvier a nommé *mastoïdien*, pour autre chose que pour la véritable écaille du temporal. Il prend part à la formation de la boîte cérébrale, il donne insertion à l'arcade zygomatique, enfin, il prête une articulation au préopercule, que nous regardons maintenant comme le véritable représentant de l'apophyse styloïde du temporal," *l. c.* p. 63. Admitting, for the sake of the argument, that the preopercular is the homologue of the stylohyal, and that it articulates with the so-called 'écaille du temporal,' which is not the case in the majority of fishes, yet this would prove more for the 'mastoid' than for the 'squamosal' character of no. 8, fig. 5. The stylohyal unquestionably articulates in many mammals with the mastoid or petromastoid, between which and the tympanic it is anchylosed in man, and it rests with M. Agassiz to demonstrate the species in which it articulates with the true squamous part of the temporal†.

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* From the remark in p. 53, t. ii. pt. ii. 'Recherches sur les Poiss. Foss.,' it would seem that the circumstance of the extension of the tympanic air-cells into the mastoid, in certain mammalia, had weighed with M. Agassiz in determining its homological characters.

† All the characters by which these highly organized fishes approximate the *Reptilia* are found, not in the highest, but in the lowest order of that class, viz. in the batrachia, and herein more especially in the salamanders. The air-bladder of *Lepidosteus* resembles the lung of the serpent in its singleness, and those of the salamander in the degree of its cellularity; some parts of the structure being peculiarly piscine. The bifid air-bladder of *Polypterus* resembles the lungs of the salamandroid menopome and proteus, in the want of cellular walls. The characteristic large bulbus arteriosus and its numerous rows of valves, which distinguish the ganoids from most other osseous fishes, are retained in the menopome, but are not present in any saurian. The anterior ball and posterior cup of the vertebræ of *Lepidosteus* are repeated in the salamander and pipa, but in no existing saurian. The labyrinthodont character of the teeth of Lepidosteus was developed to its maximum in the great extinct reptiles (*Salamandroïdes*, Jäger), which, by their double occipital condyle, dentigerous double vomer, and biconcave vertebræ, were essentially *Batrachia*, not *Sauria*; and which combined characters now found only in the lower salamandroid *Batrachia*, with dental ones borrowed from fishes, and but feebly manifested by the most fish-like of saurians (*Ichthyosaurus*). All the so-called sauroid fishes retain the characteristic piscine articular concavity on the basioccipital for the atlas: it is, however, very shallow in the polypterus; and is also extended transversely, with the lateral borders or angles so prominent, that, as M. Agassiz well remarks, "it needs very little to change this transverse articulation with its two lateral ridges into two distinct articular condyles," *l. c.* p. 71. But this would convert, *pro tanto*, the polypterus into a batrachian, not into a saurian. So far as the character of a single convex occipital condyle is valuable as a mark of affinity to the *Sauria*, it is present in a fish of a different order from the ganoids, and with much fewer approximations in other respects to the reptilian class, viz. in the *Fistularia tabaccaria*. There remains, therefore, only the character of the enamelled scales which the polypterus and lepidosteus present in common with all the lower organized ganoids, and which to a certain extent resemble the bony scutes of the crocodilia. If the deposition of calcareous matter in and upon the skin were not essentially a retention of a very low type of skeleton; if it were not presented by

With regard to the connection with the suborbital chain of ossicles, which M. Agassiz regards, with Geoffroy, as the jugal or zygomatic arch, even admitting such connection to be the rule and not the exception, all its force as an argument in favour of the squamosal character of no. 8 will depend on the ultimate decision of comparative anatomists as to the respective claims of the upper and lower zygomata in the macaw's skull, for example (pl. 1, fig. 1), to a special homology with the zygomatic arch in man and other mammals. The orbit in the bird cited, as in other *Psittacidæ*, is circumscribed below by a bony frame continued from the lacrymal (73) to the postfrontal (12), and thence to the bone (8) which I regard as the mastoid. Below this frame, the slender bone, considered by Cuvier as the jugal, and by me as the coalesced jugal (26) and squamosal (27), extends from the maxillary (21) backwards to the tympanic (28), and forms a second arch or zygoma. According to the Cuvierian and generally-received view of the homology of no. 8 in the bird, the bridge which it sends forward over the temporal fossa to join the above-described inferior boundary of the orbit, in the macaw, would be the zygomatic process; and that boundary would be what M. Agassiz calls its homologue in fishes, viz. the jugal or 'arcade zygomatique.' But what then is the parallel zygomatic arch below (26, 27), con-

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many fishes of different grades of organization, and by some, as the sturgeons and siluroids, *e. g.* under a scattered arrangement, more like that in the crocodiles than is seen in the scale armour of the typical ganoids, it might have some weight in proving the affinity of such ganoids to the highest order of reptilia; but, viewing this character under all its relations, I am not disposed to regard it as establishing that affinity more directly, than it would the affinity of the crocodile to the mammalian genus *Dasypus*. It is for the reasons above assigned that I have been accustomed to treat, in my Lectures, of the anatomical characters of the group represented by the *Polypterus* and *Lepidosteus*, as those of a *Salamandroid*, rather than of a *Sauroid* family of fishes; the characters being carried out in the direction of the batrachian order by the remarkable genera *Protopterus* and *Lepidosiren*.

* More properly 'otocranial,' in lepidosteus at least.

† In my notes on the osteology of Mammalia, I find that the stylohyal sometimes articulates with the petrosal, sometimes with the mastoid, exclusively, as in most mammals, sometimes with the tympanic, sometimes with the paroccipital process: but no instance is recorded of its articulation with the squamous portion of the temporal.

necting the maxillary with the tympanic, and marked $s^{m'}$ in fig. 7, taf. i. of Dr. Hallmann's monograph? If Cuvier had been correct in regarding no. *8* as the squamosal, the name 'jugal' ought to have been transferred from the lower zygoma to the upper one (pl. 1, fig. 1, *26*) connected with such squamosal in the macaw: and with a like consistency the name 'jugal' ought to have been retained for the suborbital chain of dermal bones in fishes (pl. 1, fig. 2, *26*), to which it had been applied by Geoffroy St. Hilaire, and to which it has been restored by M. Agassiz. But, in truth, there may be clearly discerned in the beautiful modification which has been adduced from the *Psittacidæ*, a proof of Cuvier's erroneous homology of the bone no. *8* in the class of birds, and at the same time of his accurate homology of the same bone in that of fishes.

Is there no significance in the fact of the bone anterior to the orbit, which we call lacrymal in man down to the lowest reptile, being constantly perforated by a mucous duct? Can we not recognize in this function and glandular relation, as in the commonly thin scale-like character of that bone, and its connections in front of the orbit, the repetition of the characters of the largest, most anterior, and most constant of the suborbitals in fishes (*ib.* *73*)? If the rest of that chain be sometimes wanting, but more commonly present in that class; if it should present the condition occasionally of a strong continuous bony inverted arch, spanning the orbit below from prefrontal to post-frontal, as in the right orbit of the *Hippoglossus* and the left orbit of *Rhombus*; ought we to lose our grasp of the guiding thread of 'connections' by being confronted with a repetition of that condition in the skulls of certain birds, caused by a continuous ossification from the lacrymal to the post-frontal, seeing that a diverging bony appendage of the maxillary arch, unknown in the class of fishes, has there established a second and true 'zygoma' below the suborbital one? The extension of the ossification from the post-frontal crus of the suborbital arch to the mastoid is, in truth, a beautiful repetition of an ichthyic cranial character, not unknown however in the reptilia; and whilst it adds a proof of the mastoidal character of no. *8* in the bird, it reflects reciprocal confirmation of the accuracy of Cuvier's determination of that bone in fishes.

The true signification and homologies of the bones in that interesting class could never have been elicited from an exclusive study of it, however extensive, detailed or profound; nor will the feeble rays reflected from anthropotomical reminiscences lend sufficient light in their determination: they can be clearly discerned only by the full illumination of the beams concentrated from all the grades of organic structure. M. Agassiz, descending to the determination of the squamosal in fishes from its characters in man, concludes that it must be the bone no. *6*, fig. 5, because that bone takes part in the formation of the inner as well as the outer walls of the cranial cavity. But this protective function is an exceptional one in the squamosal (fig. 6, *27*); it is peculiar to that bone only in one class, and, as we have seen, is not constant even there; whilst, on the other hand, the mastoid is recognizable from the inner surface of the cranial walls of the highest mammal (in the human cranium where it is impressed with the fossa sigmoidea, fig. 6, *8*), and in a still greater degree in that of the lowest mammal (*Echidna*, fig. 12, *8*); whilst in almost every mammal, by its coalescence with the outer surface of the petrosal, it closely repeats the protective character in relation to the external semicircular canal, which it presents in fishes,—a function which is altogether foreign to the squamosal in every mammal. I have dwelt thus long, perhaps tediously, and it may be thought unnecessarily, on the true characters and homologies of the petrosal and mastoid, because their determination is essential to, and, indeed, involves that of the squamosal and other dismemberments of the human temporal bone; and we cannot climb to the higher generalizations of anatomical science, except by the firm steps of true and assured special homologies. There are more important subjects than homologies, no doubt; but nothing is more important than truth, in whatever path we may be in pursuit of her.

Orbitosphenoid.—As evidence will be given in the section on 'General Homology' that both squamosal and tympanic belong to a quite distinct category of bones from the parts of the 'temporal' which have just been discussed. I shall proceed next to the neurapophyses that precede the alisphenoid.

As the determination of this bone (6 in all the figures) involves that of the orbitosphenoid (10), which has rarely been mistaken* for any other bone than 6, there remains little to be added in proof of its homology after what has been advanced respecting the alisphenoid. The most constant character of the orbitosphenoid is its relation to the optic nerve, which either perforates or notches it, whenever the ossification of the primitive cartilage or membrane holding the place of the bone is sufficiently advanced; which is not always the case in fishes, especially those with broad and depressed heads, and still more rarely in lacertine saurians. The recognition of the orbitosphenoid is also often obscured by another cause, viz. the tendency in the class *Reptilia*, and especially in ophidians and chelonians, to an extension of ossification downwards into the primitive membranous or cartilaginous neurapophysial walls of the brain-case, directly from the parietal and frontal bones.

In the fishes with ordinary-shaped, or with high and compressed heads, the orbitosphenoids are usually well-developed: they are, however, represented by descending plates of the frontal in the garpike; and they are, like the alisphenoids, mere processes of the basisphenoid in the polypterus, which thus offers so unexpected a repetition of the human character of the corresponding parts†. In the cod (fig. 5, 10) they are semielliptic, raised above the presphenoid (9), suspended, as it were, between the alisphenoid (6) and the frontal (11), and bounding the sides of the interorbital outlet of the cranium: the optic nerves pierce the unossified cartilage closing that aperture, immediately beneath the bone itself. In the malacopterous fishes with higher and more compressed heads, the orbitosphenoids are more developed; they are directly pierced or deeply grooved by the optic nerves, and are pierced also by the 'nervi pathetici' in the carp. The crura of the olfactory ganglions (rhinencephala) pass out of the interorbital aperture of the cranium by the upper interspace of the orbitosphenoid, into the continuation of the cranial cavity which grooves the under surface of the frontal, in their course between the orbits to the prefrontals. The orbitosphenoids protect, more or less, the sides of the prosencephalon; and this function, their transmission of the optic nerves, their anterior position to the alisphenoids, and their articulation above with the frontals, establish their special homology from the fish up to man.

In certain fishes a distinct centre of ossification is set up in the median line of the fibrous membrane or cartilage, closing the interorbital aperture of the cranium, below the orbitosphenoids, and extending forwards as the interorbital septum. The bone (represented in pl. 1, fig. 5, and in outline in cut 5, at 9') extends downwards to rest upon the sphenoid (5) or presphenoid

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* Geoffroy in his memoir on the skull of birds (Ann. du Mus. x.), indicates the orbitosphenoid at P, fig. 2, pl. 27, as the 'rocher': and Cuvier describes it as part of his 'os en ceinture' in anourous batrachia.

† Agassiz, Recherches sur les Poissons Fossiles, ii. p. 38.

(9), and bifurcates, as it ascends, to join and prop up the elevated orbitosphenoids in the perch and carp (not in the cod). The relations of this ossicle are precisely those of the part forming the conjoined bases of the orbitosphenoids in mammals, and usually called the 'body of the anterior sphenoid,' in them; though this is developed from two distinct centres. In the young whale I found it supported by a direct extension of the basisphenoid forwards, which joins the backwardly prolonged vomer, as in fishes. The common base of the orbitosphenoids is peculiar, as a distinct bone, so far as I know, to fishes. It has been called by Bojanus* the 'basis alarum minorum sphenoidei seu rostrum sphenoidei'; by Geoffroy 'entosphénal'; and by Cuvier 'le sphénoïde antérieure.' M. Agassiz opposes these determinations by the following remarks, founded on the embryological researches of the ingenious Dr. Vogt:—"In fishes with a short and thick muzzle, the cartilaginous embryonal plate ('plaque faciale' of Vogt), which serves as the base of support to the prosencephalon and the nasal fossæ, is transformed into an independent bone, "se transforme intégralement en os." It is then, he says, "represented by the cranial ethmoid (le *sphénoïde antérieure* of Cuvier), an azygous bone, 'os impair,' short, of an almost square form, in which are pierced the canals for the transmission of the olfactory nerves. But in the fishes with elongated muzzles, and of which the eyes in place of preserving their primitive lateral position at the sides of the mesencephalon are carried forwards in advance of the cranium between that and the nasal fossæ, the relations of the 'plaque faciale' are necessarily altered: part of the plate remaining in its primitive situation is transformed into the 'cranial ethmoid,' the other part is carried forwards, but is never transformed into a distinct bone: it remains cartilaginous as the nucleus of the muzzle; or if, indeed, the ossification of the muzzle is completed, it disappears by virtue of the progressive encroachment of the exterior ossification. This is the reason why fishes have never a true 'nasal ethmoid' (the bones called ethmoid by Cuvier are the nasals), but only a cranial ethmoid†." Influenced by the deservedly high authority of M. Agassiz, I adopted his homology of the bone 9' in the 'Hunterian Lectures on Vertebrata,' delivered in 1844. But since the notes of those lectures were printed, having been charged with the formation of a new Osteological Catalogue of the Hunterian Museum, I have carefully reconsidered this question. Passing over, for the present, the assertion that the homologue of the 'nasal ethmoïde' does not exist in fishes, I would first observe, that if the orbital aperture (or what appears to those who deem the rhinencephalic crura to be olfactory nerves, the anterior aperture) of the cranium were homologous with the aperture closed by the cribriform plate in man, then any bony bar or plate tending to close that aperture might be held to be homologous with the cribriform plate or crista galli of the ethmoid: but the interorbital aperture of the cranium is always bounded laterally, in fishes, by the orbitosphenoid; and the rhinencephala and their crura extend forwards, to a considerable distance in most fishes, before the olfactory nerves sent off from the rhinencephala escape by those perforations in the prefrontals, which are the true homologues of the single foramina of the olfactory nerves in the so-called ethmoid of birds, and of the cribriform foramina in mammals. The interorbital groove or canal in the skull of fishes, which is continued from the presphenoidal or interorbital aperture to the prefrontal foramina, is as essentially a part of the cranial cavity as is that contracted anterior olfactory chamber of the cranium of mammals, which, in the thylacine, for example, extends forwards, from where the orbitosphenoids sustain the frontals, expanding, to where the frontals and the modified prefrontals (ethmoid) form the actual anterior boundary wall of the cranial cavity; the chief distinction between the condition of this boundary in the mammal and the fish, being, that whereas it is perforated by numerous apertures in the mammal, the olfactory nerves in the fish escape each by a single foramen or groove in the homologous bones. As beautiful as true was that clear perception by Bojanus of the homology of the simply perforated prefrontal of the fish, with its sieve-like homologue in the class in which the olfactory sense reaches its maximum of development and activity, and modifies all around it. The coalesced bases of the orbitosphenoids, forming the anterior boundary of the bed of the optic chiasma, answer to the separate ossification called 'ethmoïde crânien' by Agassiz, in fishes: it has the same relation with that contracted area of the cranium answering to the interorbital aperture of the cranium in fishes, which the so-called cranial ethmoid (entosphenoid) presents in fishes; and this same entosphenoid (fig. 5, 9') has as little relation to the formation of the canals pierced by the olfactory nerves in fishes, as the orbitosphenoid has in mammals. The olfactory, rhinencephalic or anterior division of the cranial cavity in most fishes has its lateral bony walls incomplete, and it opens freely, in the dry skull, into the large orbital chambers below, which are then said to have no septum: we see a similar want of definition of the cranial cavity in relation to the great acoustic chambers in most fishes. But in mammals the orbits are always excluded from the rhinencephalic, or olfactory compartment of the cranium*; and a like exclusion obtains in some of the highly organized ganoid fishes and in the plagiostomes. As the prosencephalic parts of the brain progressively predominate, and the rhinencephalic parts diminish, in the higher mammals, the compartment of the cranium appropriated to the latter loses its individuality, and becomes more and more blended with the general cavity. In the elaborate 'Iconography of Human Anatomy' by Jules Cloquet, for example†, the small peculiarities of the 'trou borgne' and the 'apophyse crista galli' are both indicated, and very properly; but the rhinencephalic or olfactory division of the cranial cavity, though defined by the suture between the orbitosphenoids and prefrontals and lodging the olfactory ganglia or rhinencephala,—so important an evidence of the unity of organization manifested in man's frame and traceable in characters, strengthening as we descend to the lowest osseous fishes—is wholly unnoticed. Thus, very minute scrutiny, conducted with great acuteness of perception of individual features, qualities highly characteristic of the anthropotomists of the school of Cloquet, being directed from an insulated point of view, prove inadequate to the appreciation of sometimes the most constant and important features of their exclusive subject.

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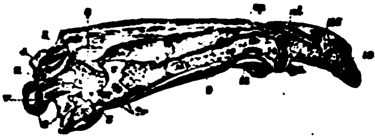
* Oken's Isis, 1818, p. 508.

† Recherches sur les Poissons Fossiles, t. i. p. 128.

Fig. 13.



Side view of cranium (*Rana boans*), nat. size.

But to return to the homology of the orbitosphenoids. In the menopome these neurapophyses are elongated parallelograms, perforated by the optic nerves, and are distinct bones. In the great bull-frog (*Rana boans*) they present a similar form (fig. 13, 10), but are confluent with the prefrontals (14): in both batrachians an unossified space intervenes between them and the alisphenoid (9). In most lizards the wider roof of the cranium, supported by the long mastoids, squamosals, postfrontals and malars, like a bony scaffolding on each side, is independent of its proper (neurapophysial) walls for support, and these retain, through the œconomy of nature, much of their primitive semi-membranous, semi-cartilaginous state. A dismemberment of the alisphenoid (which may be discerned as a process of that bone in the piscine genera *Xiphias*, *Sphyræna*) props up the parietal upon the pterygoid, so like a post or pillar, that the name 'columella' may well be retained for it. At the sides of the membrane forming the orbital aperture, rudiments of the orbitosphenoids may be seen in most lacertia: I find them, *e. g.* in the form of a slender osseous filament on each side, slightly bent inwards and bifurcate above, in a large Australian lizard (*Cyclodus gigas*). In the crocodile (figs. 9, 20, and 22, 10) the orbitosphenoids attain their maximum of development, but retain all their typical characters: they bound the orbital aperture of the cranium; are notched below, as in many fishes, by the optic nerves (*op*); are perforated by the pathetic and other orbital nerves at the 'foramen spheno-orbitale' (*s*); they protect the sides of the prosencephalon; support above the frontals (and by their backward development also the parietals); and they rest below upon a peculiar development of the presphenoid (9), which seems to answer to the entosphenoid in fishes.

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* This is not to be confounded with the olfactory chamber itself, lodging the organ of smell.

† Manuel d'Anatomie Déscriptive, 4to, Atlas, pl. 8, fig. 2.

Some salient points of resemblance between the cranial organization of fishes and birds have elicited remarks from more than one comparative anatomist. Not to dwell upon the more obvious correspondence arising out of the mobility of the upper jaw, chiefly through its connection with the pedicle of the lower jaw, I may indicate the overhanging position of the orbitosphenoid (figs. 8, 23, 10), raised high above the presphenoid (9), at the beck part of the interorbital septum: we see exactly the same position of the orbitosphenoid in many fishes. Cuvier accurately represents it in the skull of the perch*. This beautiful trait of unity of organization is completely put out of sight by the false homology of the orbitosphenoid in fishes with the alisphenoid in birds and mammals. The progressive recession of the orbitosphenoid and alisphenoid, as we descend from mammals to fishes, transfers indeed their characteristic nerve-notches or foramina from their posterior to their anterior margins. But the notch (*op*, fig. 8) at the posterior margin of the orbitosphenoid in the bird for the escape of the optic nerve by a foramen common to it and the nerves of the orbit, is not less significant of its true homology than is the anterior notch in the crocodile or fish; the osseous connections with the sphenoid below, with the frontal above, and with the alisphenoid behind, being the same.

Prefrontals.—If the cranium of a cod-fish be bisected horizontally and longitudinally, its most contracted part will be found at the upper part of the interorbital aperture, bounded by the orbitosphenoids, which mark the division between the prosencephalic and rhinencephalic compartments of the cavity: the latter extends as a triangular channel or groove on the under part of the frontal, opening below into the orbits, gradually expanding as it advances forwards, and dividing into two canals, which diverge to the interspaces left on each side of the nasal, between it and the bones (fig. 4, 14), that, meeting behind the anterior expanded end of the nasal, bound the anterior extremity of the true and entire cranium. The diverging canals of the rhinencephalic compartment are formed by the two bones in question: the rhinencephala or olfactory ganglions are sometimes lodged at the extremities of these canals, and they send out the olfactory nerves by the apertures formed between the bones 14 and 15, which then ramify upon the vascular olfactory sacs, supported by the bones 15, fig. 5. For the arguments by which the olfactory ganglions in the cod are shown to be homologous with the olfactory ganglions that rest upon the cribriform plate in man, and by which the medullary cords or crura connecting them to the rest of the brain are shown to be homologous with the so-called 'olfactory nerves' in the human cranium, and for the general homology of both as primary divisions and peduncles of the encephalon, the reader is referred to Dr. Desmoulins, 'Anatomie des Systèmes nerveux des Animaux à Vertèbres,' 1825, 8vo. t. i. p. 169; to Mr. Solly's excellent treatise 'On the Human Brain,' 1836, p. 78; and to my 'Lectures on the Vertebrata,' 1836, p. 184. I there adopt the expressive name applied by MM. Vogt and Agassiz to this most anterior of the four primary divisions of the brain of fishes, and apply to the peduncles of the 'rhinencephala,' which are frequently of great length in fishes, the name of 'rhinencephalic crura,' since they are serially homologous with the prosencephalic or cerebral crura; and I call that division of the cranial cavity which specially lodges these crura and their lobes the 'rhinencephalic' chamber or compartment. The right appreciation of the above essential characters of the most anterior division of the brain and brain-case is indispensable to the accurate pursuit of the homologies of the bones 13, 14 and 15, whose development, especially of the pair no. 14, is governed by that of the rhinencephalon. In man the all-predominating cerebrum, overarching the mesencephalon and epencephalon behind, and the rhinencephalon in front, so modifies the surrounding cranial bones as to obliterate every part of the rhinencephalic division, save the terminal fossa that immediately supports the so-called 'olfactory ganglia,' which fossa seems, as it were, to be unnaturally drawn in and blended with the great prosencephalic chamber, by reason of the enormous outswelling development of the proper spines or roof-bones of that chamber, the frontals. Still, even here, through the absence of any commissural band connecting together the rhinencephala, a fibro-membranous process of the endoskeleton extends between them, and into this septum ossification extends from below, called the 'crista galli.' In the cod-fish the homologous partition between the rhinencephala is cartilaginous, and it extends some way back between their crura, not being opposed by a coextended overhanging cerebrum with great transverse commissures. In many fishes (e.g. *Xiphias*, pl. 1, fig. 5) the outlet of the olfactory nerves, which notches the inner side of no. 14 in the cod, is converted into a foramen (*ib. ob.*) by the extension of ossification around the mesial surface of the nerves. Where the olfactory nerves are sent off from the ganglions in great numbers (e. g. *Raia*), they perforate a membrane before reaching and ramifying upon the vascular pituitary sac. In man, the homologous membrane, or basis of the olfactory capsules, is ossified, and called from its numerous apertures the cribriform plate. The holes which these cribriform plates fill up are homologous with the foramina, or grooves forming the outlets of the olfactory nerves in the bones no. 14 in fishes (figs. 4 and 5).

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* Histoire des Poissons, pl. ii. figg. i. vii. 14.

The grounds for this homology are so plain that we cannot be surprised that they should have been early appreciated, as *e. g.* by the painstaking and philosophic Bojanus in 1818*. I never could comprehend the precise meaning of the statement with which Cuvier opposed his view:—"M. Bojanus, partant sans doute du trou qu'il a dans plusieurs poissons pour le nerf olfactif, en fait une lame cribleuse de l'ethmoïde; mais cette opinion, qui n'a pas ce soutien dans toutes les especes, est réfutée d'ailleurs par les autres rapports de cet os avec les os voisins†." Cuvier seems to have thought the ground of Bojanus's opinion to be cut away by the fact that in the cod and some other fishes the olfactory nerves groove instead of perforate the bones no. 14. But the trigeminal still determines the alisphenoid, whether it perforates or notches that neurapophysis in its escape: the relation of the alisphenoid to the division of the *5th*, including the gustatory nerve, and that of the orbitosphenoid to the nerve of sight, are not more constant than is the relation of no. 14 to the nerve of smell. The differences of connection of no. 14—'les autres rapports'—are not specified by Cuvier, and I know none that affect its essential character.

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* Isis, heft iii. p. 503.

† Histoire des Poissons, i. p. 236.

No. 14 is however the most anterior of the neurapophysial or lateral bones of the true cranium, and is in relation with the anterior terminal division of the encephalon and with the first or anterior terminal pair of nerves. Like all extreme or peripheral parts, it is subject, as we should be prepared to find it, to a greater extent and variety of modifications than the more central neurapophyses. The difference between its connections in the fish and that of the cribriform plates and their sustaining basis in man may therefore be expected to reach the extremes of possible homology. It will be interesting to inquire whether there are intermediate modifications by which the nature of that difference may be appreciated, and how many of such links are permanently retained in the intervening species.

We might anticipate the smallest amount of departure from the fundamental vertebrate type, as respects form, size and connections of the bones in question, in that class where the principle of vegetative repetition most prevails and the archetypal plan is least obscured by teleological adaptations. Adopting the name modified from the phrase applied to these bones by Cuvier in those vertebrata in which they present their most typical characters, we find the 'prefrontals' in all bony fishes resting below upon the vomer (figs. 4 and *5*, 14) and on part of the presphenoid (9), sustaining by their mesial and upper surfaces the nasal (15) and fore-part of the frontal (11), affording the whole or part of the surface of articulation for the palatine (20) or the palato-maxillary arch, and giving attachment exteriorly to the large suborbital or lacrymal bone (pl. 1, fig. 2, 73), when this exists. Besides their protective functions, in relation to the olfactory ganglions and nerves, they close the cranial cavity and bound the orbits anteriorly. The most constant and characteristic connections appear to be with the vomer, nasal, palatine and frontal. In the murænoid fishes, where confluence begins to prevail in the cranial bones, we find that the prefrontals coalesce with the vomer and nasal, not with the true frontal. This fact, though not of a class materially affecting relations of homology, is not devoid of significancy in regard to the real character of the bone usually described as one of the 'deux démembremens du frontal*.' A clew not to be neglected in tracing the homologies of the prefrontals is their histological progress, although the value of such embryonic characters has been overrated and their application sometimes abused. The substramen of their ossification, like that of the exoccipitals, mastoids and post-frontals, is a cartilaginous mass, a part of that which M. Dugés has called 'cartilage cranio-faciale,' and M. Vogt 'plaques protectrices latérales.' The frontals and parietals, being ossified in supra-cranial fibrous membrane with so rapid and transitory a cartilaginous change as to have escaped general recognition, have been, on that account, rejected from the vertebral or endo-skeletal system of bones by Dr. Reichert, and with as little real ground as the rejection of the vomer and sphenoid from the same system, because they are ossified in membrane extended from the under and fore-part of the sheath of an evanescent subcranial 'chorda dorsalis,' like the homologous basal ossification beneath the coalesced anterior abdominal vertebra of the siluroids.

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* Agassiz, *op. cit.* i. p. 128.

M. Dugès, who has accurately figured the 'cranio-facial' cartilage of a gadoid fish in pl. ii. of his valuable Monograph[*], gives as accurate a figure of the same cartilage in the *Rana viridis* (pl. i. figs. 6, 7, of the same work), out of which has been ossified a bone which transmits the olfactory nerve to its sense-capsule: this bone (14 in the figures cited) rests below upon the divided vomer and on the end of the presphenoid, sustains above the nasal and fore-part of the frontal, affords an articular surface on its outer part for the palatine, and only fails to repeat every characteristic connection of the prefrontals in fishes, because (as likewise happens in certain of that class) there is no lachrymal bone developed in the *Batrachia*. The sole modification of any consequence tending to mask the homology is this; that whereas we find in many fishes ossification extending into the persistent part of the craniofacial cartilage connecting, whilst it separates, the prefrontals, so as to circumscribe the canals for the transmission of the olfactory nerves, such ossification proceeds in the anourous batrachia to anchylose the prefrontals with each other, and convert them into a single bone. This difference however sufficed with Cuvier to make of it a new and peculiar bone—an 'os en ceinture[†].' It would have been as reasonable to have given a new name to the supraoccipital in the *Lepidosteus*, because it is divided in the middle line instead of being single, or to the frontal in the species where it is single instead of being divided, or to the vomer in the frog because it is double instead of single, or to the exoccipitals in the same reptile, which manifest the same mesial and annular confluence as the prefrontals. But, adds Cuvier, in reference to the single bone (fig. 13, 14) resulting from this modification, "Je ne l'ai pas trouvé divisé, même dans des individus très-jeunes qui avoient encore un grand espace membraneux entre les os du dessus du crâne." Nor did the great anatomist ever find the rudiments of the radius and ulna distinct at any period of development of the single bone of the *Batrachia*, which he nevertheless rightly describes as representing both bones of the fore-arm: nor did he ever find a division of the single parietal in the embryo crocodile, which he equally well recognized, nevertheless, as the homologue of the two parietals, which in most fishes have been subject to greater modifications in their connections and relative position than the single prefrontal presents in the anourous batrachia. These are not the only instances where relations of homology are by no means obscured, nor ought to be, by reason of the confluence or even connation[‡] of essentially distinct elements. The capsule of the olfactory organ, partly protected by the anterior infundibular expansions of the connate prefrontals, undergoes no partial ossification homologous with the 'turbinal' (19, fig. *5*) of fishes, but remains cartilaginous, like the sclerotal and petrosal.

The prefrontals, however, are not only connate with each other in the frog, but coalesce with the contiguous neurapophyses—the orbitosphenoids (10, fig. 13). And this modification has led Cuvier, notwithstanding the connection of the bone 10 with the presphenoid below, with the frontal above, and with the prosencephalon, optic nerve (*op*) and orbit, to characterise the batrachian skull as having "un seul sphénoïde sans ailes temporales ni orbitaires;" the true and distinct 'alisphenoid' (6, fig. 13), with its typical connections and nerve-perforations (*tr*), being described as the potroeal, 'rocher[*].' But the real difficulties which beset the quest of general truths in comparative osteology are such that we may well dispense with any over-statements of the amount of deviation from the cranial archetype which much-modified skulls like those of the anourous batrachia may present. Fortunately the light which the development of such skulls throws upon their mature characters, is aided by the persistent larval stages manifested by the perennibranchiate species.

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[*] Recherches sur l'Ostéologie, &c. des Batraciens, 4to, 1835.

[†] Ossemens Fossiles, 4to, t. v. pt. ii. p. 387. He had before applied the name of 'ceinture osseuse' to the scapular arch in fishes.—Leçons d' Anat. Comp. i. (1800) p. 232.

[‡] I use these terms in the same definite sense as the botanists; those essentially distinct parts are *connate* which are not physically distinct at any stage of development, those united parts are *confluent* which were originally distinct.

In the menopome, for example, the prefrontals remain distinct, both from each other and from the orbitosphenoids[†], their characteristic connections and functions being the same as those of their coalesced homologues in the frog, except that they are notched, instead of being perforated by the olfactory nerve, which grooves their inner border, as in the cod and some other fishes. Cuvier just hints at the possibility of his 'os en ceinture' in the frog representing "à la fois le frontal principal et l'ethmoïde[‡]," or as having an equal pretence to one or the other name.

The suture, however, which marks the limits between the frontal 11 and parietal 7 is persistent in the menopome, and indeed in all batrachians but the anourans; and even in the very young larvæ of these, Cuvier admits (and the observations of M. Dugès warrant the admission) "que l'on sépare une partie postérieure de forme ronde de l'antérieure qui est allongée" (*Ibid.* p. 387). The permanently distinct frontals present a similarly elongated form in the urodeles, and are therefore recognized by Cuvier in the salamander, *e.g.* at *c*, pl. xxv. fig. 1, *op. cit.*; in the newt, pl. xxvi. fig. 6; in the menopome, fig. 4; in the axolotl, pl. xxvii. fig. 24; in the siren, *ib.* fig. 2; and in the amphiuma, *ib.* fig. 6. In all these crania the true frontals are indicated by the same letter *c*; in none of them do they close the cranial cavity or bound the orbits anteriorly, or are perforated by the olfactory nerves, or articulate with the vomer below, or perform any of the essential functions, or combine the characteristic connections of the prefrontals of fishes, all of which concur in the 'os en ceinture.' But the frontals do present the chief connections and occupy the relative position of the anterior half of the bone (7 and 11, fig. 13) which Cuvier calls the parietal in the frog. The evident tendency to coalescence of essentially distinct bones which pervades the skeleton in the adult anourans greatly diminishes the difficulty, through the loss of the suture between the parietal and frontal, of recognizing the homology of the latter bone, which, with that exception, not only repeats the characters of the frontals in fishes, but of those in most tailed batrachians.

Next, then, with regard to the ethmoid, the second of the two bones to which Cuvier restricts the choice of the homologues of the 'os en ceinture,' no. 14. No name has been applied more vaguely or with a less definite meaning than this same 'ethmoïde.' In the sense in which Cuvier would permit its application in the present instance, it is a bone which forms the anterior and antero-lateral walls of the cranium, defends the rhinencephala and transmits the olfactory nerves, but is altogether distinct from and posterior to the capsules of the organs on which those nerves are ramified. In the crocodile Cuvier restricts the term 'ethmoid' to the cartilaginous laminæ, capsules, or supports of the olfactory ramifications after the nerves have left the cranium. In mammals the ethmoid is made to include both the bones that close the cranium anteriorly, support the rhinencephala, give exit to the olfactory nerves, and those which defend and sustain the enormously developed and complex superior parts of the organ of smell*. Whilst this confusion is permitted to vitiate osteology, it is plain that no intelligible homological or other proposition can be predicated of the 'ethmoid.'

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[*] *Op. cit.* p. 386.

[†] The menopome, which represents a gigantic tadpole of the tailless batrachia, manifests a beautiful conformity to the general type, and well illustrates the real nature of the apparent deviations which take place in the course of the remarkable metamorphoses of the anourans. At first sight the orbitosphenoids seem to be barred out from their normal connection with the frontal by the junction of the parietal with the prefrontal in the menopome, as appears, for example, in the figure given by Cuvier in the 'Ossemens Fossiles,' v. pt. ii. pl. xxvi. fig. 4, where *c' h* divides *c* from *u*. Remove, however, the prefrontal *h* from the parietal *c'* (which may be readily done, the suture, which is not indicated in the figure cited, being persistent), and the anterior and mesial half of the orbitosphenoid (*u*) is then seen extending inwards (mesiad), beneath the parietal and prefrontal, to join a triangular surface formed by a descending process from the middle of the outer edge of the frontal.

[‡] *Op. cit.* p. 388.

When Cuvier, with reference to the hypothetical possibility of the homologue of the frontal forming part of the bone 7 and 11 in the frog, adverts to the second mode of bringing the 'os en ceinture' into the ordinary category of cranial bones, by viewing it as the 'ethmoïde,' he adds, that it would then be "un ethmoïde ossifié, se que sera une grande singularité" (*ib.* p. 388). Here it is obvious that the predominating idea of the ethmoid was that presented to his mind by the capsules of the olfactory organ in the crocodile and other reptiles, which he had so called, and which are wholly or in great part cartilaginous. But the parts of Cuvier's ethmoid in birds and mammals, which are in functional and physical relation with the cranial cavity, rhinencephala and olfactory nerves, are ossified: the bone, also, to which he gives the name 'ethmoid' in fishes (fig. 5, 15), is ossified; and, what is more to the purpose, the bones (14) in fishes, ophidians, chelonians and saurians, which repeat the essential characters of the batrachian 'os en ceinture,' are likewise ossified.

General homology teaches that the bone or bones in relation to the defence of the rhinencephala and the transmission of their nerves belong to one class, and that the parts of the skeleton, whether membranous, gristly or bony, which form the capsule or sustain the olfactory organ itself, belong to another and very different class of parts of the skeleton. But, not to anticipate what belongs more properly to a subsequent chapter of this work, observation shows the two parts to be physically distinct in all vertebrates except mammals, and to be distinct in the fœtus of these. Whether we restrict the term 'ethmoid' to the neurapophysis or to the sense-capsule (which in mammals includes the 'conchæ superiores' and cells of the ethmoid), the term must be applied arbitrarily in its extended or homological signification, since the neurapophysis dismisses the nerve, not by a 'sieve-like' plate, but by a single foramen or groove in all the vertebrates below mammals. The multiplied foramina in the neurapophysial or cranial part of the anthropotomical 'ethmoid,' whence that name, as well as the special designation of the part called 'lamina cribrosa,' are modifications peculiar to the mammalian class, but not constant here, and they form no essential homological character of the bone in question. It appears to me preferable, since we have two essentially distinct parts of the skeleton combined in the mammalian and human ethmoid, to restrict the term ethmoid to the part which appertains to the sense-capsule, *i. e.* which is directly concerned in the support of the membrane and cells of the olfactory organ.

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* Objecting to Oken's idea, that the prefrontal in the crocodile was homologous with the part of the ethmoid called 'os planum' in anthropotomy, Cuvier says, "Or l'os planum ne paroît jamais sur la joue; il ne se montre plus dans l'orbite à compter des makis si ce n'est un petit point dans les galeopitheques et dans quelques chats. Dans tous les autres mammifères l'ethmoïde est entièrement enveloppé et caché par le palatin" (note that significant connection) "et par le frontal et spécialement par cette partie du frontal dont il est maintenant question et qui se détache dans les ovipares. Le véritable ethmoïde est enveloppé de la même manière dans le crocodile, quoique presque toutes ces parties restent cartilagineuses."—Ossem. Foss., v. pt. i. p. 73.

But leaving for the present the question of names, and returning to things, let us pursue our search and comparisons of the bones which continue in the higher classes to repeat the essential characters of those called 'prefrontals' in fishes. Were it necessary to add to the reasons above assigned for regarding no. 14, fig. 13, as the homologues of 14 in the fish, notwithstanding they are connate in the batrachian, I would cite the structure and relations of those bones in the sword-fish. The whole of the anterior part of the extensive interorbital space is occupied by the prefrontals (Pl. I. fig. 5, 14) which join each other at the median line by an extensive vertical cellular surface: they form the anterior border of the orbit, and the posterior wall of the nasal fossa; they close the cranial cavity anteriorly, and each transmits the olfactory nerve to the capsule by a central foramen. They are almost covered by the frontals (11) above, which they support by a broad flat surface; a very small portion only appearing on the upper surface of the skull at the anterior angle of the orbital ridge. Were the frontals separated, the prefrontals would then appear, as in the frog, at the median line: were the suture between the two prefrontals to be obliterated in *Xiphias*, an 'os en ceinture' would be produced like that of the frog. The nasal bone of the sword-fish, which Cuvier calls 'ethmoïde,' presents a cellular structure of its base (15, *ns n*) designed to break the force of the concussion arising from the blow which is delivered by the 'sword.' But the prefrontals manifest more extensively this peculiar cellular structure, which Cuvier well says, "l'on prendrait presque pour les cellules de l'ethmoïde d'un quadrupède*."

Cuvier, not perceiving or not appreciating the grounds of the homology of the 'os en ceinture' with the prefrontals, describes the divided nasal (15, fig. 13) in the batrachia as the 'frontaux antérieures'; and reciprocally, having called the bones in fishes, homologous with the bone 14, (which he thought might represent the ethmoid in the frog) 'frontaux antérieures,' he gives the name 'ethmoïde' to the bone 15, fig. 5, whether single or divided, in fishes. It is not necessary to add anything to the arguments by which M. Agassiz has sustained the conclusion of Spix, that Cuvier's 'ethmoid' in fishes is the 'nasal.' And it needs, I think, only to compare the connections of the bones 15, fig. 13, with either the single or the divided nasals in fishes, and to glance at the obvious homology of the bones *h* in Cuvier's pl. xxiv. fig. 1—6, with the bones *g g* in figs. 4 & 6 of pl. xxvi. ('Ossemens Fossiles,' t. v. pt. 2), to ensure the acceptance of the conclusion, that his 'frontaux antérieures' in the frog and the other anourans are the true nasal bones.

The membranous and cartilaginous basis of the lateral walls of the cranium, especially of its anterior compartments (prosencephalic and rhinencephalic), are incompletely ossified in all lacertian Sauria. The orbitosphenoids are represented in most by small styliform ossicles ('Ossemens Fossiles,' t. v. pt. 2, pl. xvi. fig. 1, *z*) bounding the anterior and inferior part of the prosencephalic chamber, and which Cuvier, who describes the true alisphenoid as the petrosal (rocher), regards as the representative of both alisphenoid and orbitosphenoid. The alisphenoid is, however, well characterized by its connections with the basisphenoid and exoccipital, with both of which it commonly becomes anchylosed; by the share which it contributes to the chamber lodging the true cartilaginous 'petrosal'; and by the notch on its fore-part for the escape of the third division of the fifth nerve.

The orbits and rhinencephalic groove are bounded anteriorly and divided from the olfactory compartments by two transversely extended and antero-posteriorly subcompressed bony columns, resting upon the palatines below, and arching upwards and backwards, expanding as they ascend, and defining externally the membranous space perforated by the olfactory nerves. These are the parts in all lizards that repeat the essential characters of the prefrontals in batrachians and fishes: they are, moreover, distinct from one another, and appear on the upper surface of the skull anterior to the frontals, and thus resume their more typical character as first displayed in fishes. In the large monitors ('Ossemens Fossiles,' v. pt. 2, pl. xvi. fig. 1, *e*) there can be no mistake as to their special homology; since they articulate with the lachrymals (*f*) (homologues of the great anterior muco-dermal suborbital bone), and also, as in the carp, with a supraorbital ossicle (*k*): but in many other lizards and in serpents they are confluent or connate with the lachrymals. In this case the external antorbital position and perforation for the mucous duct distinguishes the lachrymal portion of the coalesced bones. In the python the broadest part of the palatine, formed by the process directed inwards and by the opposite one sent outwards for the suspension of the maxillary, articulates with the under surface of the prefronto-lachrymal bone; and the inner part of the true prefrontal portion is notched by the olfactory nerve in its passage to the capsule supported by the ossified turbinal*.

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* Hist. des Poissons, t. viii. p. 194.

The bones, which more resemble the anchylosed prefrontals in the frog, are the frontals of the python; but the resemblance is confined to one character only, and that an exaggeration of a character common to the frontal bones of many birds, and of the ornithorhynchus among mammals, viz. a development of a median bony partition from the line of the frontal suture into the median interspace of the encephalon. In the python each frontal sends down at the fore-part of this suture such a partition, which is therefore double, as the falx essentially is in man and the mammalia, in which it retains its primitive histological condition of a fibrous membrane. The ossified laminæ of the falx in the python bend outwards and coalesce below with the external or orbitosphenoidal plates of the frontal, and thus surround the lateral divisions of the fore-part of the brain (rhinencephala), which are drawn back in the progress of the concentrative movement of the cerebral centres, so as to occupy the prosencephalic segment of the cranium, the prosencephalon being, in like manner, protected chiefly by the mesencephalic bony arch. The change is precisely analogous to that which takes place at the opposite extremity of the neural axis in higher animals. In the python every segment of the spinal chord retains its primitive relation to the segment of the endoskeleton, through which it transmits its pair of nerves. In the mammal the concentrative movements of the spinal chord draw its hinder segments in advance of their proper vertebræ, and the primary relation is indicated by the nerves which these vertebræ continue to transmit, and by which alone we are guided from the segment of the endoskeleton to that of the neural axis which originally governed its development.

Accordingly, at the anterior end of the skeleton, we trace the relation of the osseous segment, which transmits the olfactory nerves to their capsule, to its proper division of the neural axis, by following those nerves back to the retracted ganglions (rhinencephala) from which they take their origin. The connections of the annular frontals of the python with the parietals and post-frontals behind, with the connate orbitosphenoids, and through them with the presphenoid below, prevent their homology being mistaken; for they are far from completely representing or repeating the essential characters of the coalesced annular prefrontals of the frog.

Not to lengthen unnecessarily this exposition of the homologues of the prefrontals (14, figs. 4 and 5) in fishes, I pass at once to the highest of existing reptiles, the crocodile. Here we find, in the dry skull, the condition of the cranial cavity in the fish beautifully and closely repeated: the prosencephalic part opens freely by the aperture bounded by the orbitosphenoids (fig. 9, 10) into the common orbital cavity (*or*), and the rhinencephalic division of the cranium is prolonged, as a groove upon the under surface of the coalesced frontals (*ib.* 11) above the orbits, expanding as it advances, until it is arrested by a boundary formed by two bones (*ib.* 14), which rest below upon the vomer and give attachment there to an ascending process of the palatines (20), which sustain by their mesial and upper expanded surfaces the nasal (15) and forepart of the frontal (11); and articulate exteriorly with the large lachrymal bone (fig. 22, 12) perforated as in the fish and lizard by a mucous duct from the orbit. They are each grooved on their inner or mesial surface (indicated by the numerals 14, in fig. 9) by the olfactory nerve, where it escapes from the cranium to spread upon the membranes sustained by the cartilaginous capsules anterior to the bones in question; below these grooves the bones (14) extend inwards and meet at the mesial line; but do not coalesce there as in the frog, nor extend their mesial union upwards, so as to convert the olfactory grooves into two complete canals. They, therefore, retain or resume much more of their primitive piscine character than do their homologues in the frog, and manifest it conspicuously by developing a subtriangular external plate which appears on the upper surface of the cranium at the anterior angle of the orbit between the frontal, the lachrymal and the nasal bones. In short, the homology of the bones 14 in the crocodile (figs. 9, 21, 22) with those so numbered in the fish (figs. 4 and 5), was quite unmistakeable; and, with the exception of Spix, all anatomists have concurred in this respect with Cuvier: only some of them have extended further and expressed differently the homologies of the bones in question.

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* In my 'Report' I was misled by the confluence of the true prefrontals with the lachrymals to view the turbinals ('cornets inférieures' of Cuvier) as the homologues of the prefrontals in the python.—Report of British Association, 1846, p. 220.

Now, bearing in mind the small brain of the cold-blooded crocodile, and the concomitantly restricted development of the spine or roof-bone in special relation with the cerebrum, viz. the frontal (11), which is aided in its secondary function in relation to the orbit by distinct supraorbital bones in all crocodiles, and contrasting the condition of the part of the brain which chiefly governs the development of the frontal bone with that of the same division of the brain of mammalia,—let us proceed to make the comparison which Cuvier recommends*, in order to trace the homologues of the crocodile's prefrontals in the mammalian class.

We place the skull of a ruminant (the red deer, *e. g.*) by the side of that of a crocodile, and delineate a suture which would detach a portion from the frontal, having the same superficial connections as the upper peripheral plate of the prefrontal has in the crocodile. It appears to be far from presenting the same figure; but most assuredly such artificially detached portion of the ruminant's frontal has not the same functions ('emploi') as the prefrontal has in the crocodile. For if we even include with the part so detached the anterior portion of the descending orbital plate of the frontal, we find it joining below the orbitosphenoid without any connection with the vomer, or any attachment to the palatine: it forms no immediate part of the supporting plate of the rhinencephalon, nor of the foramina for the exit of the olfactory nerves. Such artificially detached portions of the mammalian frontal are entirely separated from each other; whilst one of the important points of resemblance between the prefrontals of the crocodile and those of the fish are the mesial approximation and junction of their descending (neurapophysial or rhinencephalic) plates—the most constant and important parts of the bones in question.

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* "Il suffit en effet de placer une tête de mammifère, de ruminant par exemple, à côté d'une tête de crocodile, pour s'assurer qu'il s'est fait ici ('du frontal antérieur') un démembrement du frontal. On pourroit, sans rien déranger, dessiner sur le frontal du mammifère la suture qui existe dans le crocodile, et on détacheroit ainsi dans le premier un frontal antérieur qui auroit la même position, presque la même figure, et absolument le même emploi que dans le crocodile."—Ossem. Fossiles, v. pt. ii. p. 73.

If the frontal of the ruminant or other mammal were expanded only at the parts corresponding with the detached bones called "frontaux antérieures" in the crocodile, there might then be a *primâ facie* probability that such expansions were connate parts, dismembered in the crocodile's skull. But the vastly increased lateral as well as anteroposterior development, and the more or less vertical convex expansion of the frontal in the highest vertebrate class, naturally indicate, in the first place, an inquiry into the concomitant modification of the nervous centres by which the development of that bone is mainly governed; and if such modification should then be found to exist, in the cerebrum, for example, which, from the ascertained correlative progress of the frontal in other classes, ought to cause or be associated with such a general development of that bone as characterises the skull in the mammalian class, it must surely be superfluous and gratuitous to explain that development by the hypothesis of a coalescence of another essentially distinct element of the cranial parietes: especially if that element be proved, by a similar tracing of its relations to the progressive development of the cerebral centres, to have as essential and exclusive a dependence upon the rhinencephalon as the frontal bone has upon the prosencephalon.

The position of the upper peripheral part of the prefrontal in the situation in which it is seen in the crocodile, is, in fact, the least constant and important of the characters of that bone. In the bull-frog, for example, the exposed part of the prefrontal is mesiad of the conjoined parts of the nasals and frontals instead of being lateral: in the sword-fish the prefrontals barely appear, and in the python they do not appear at all, upon the upper surface of the skull; but they retain in each their more typical neurapophysial position, with all their more constant and essential characters. The enormously developed frontal of the mammal masks these characters, and usurps the less constant and least important one, viz. superficial position, on which alone Cuvier insists as proving the prefrontal of the crocodile, with its complex functions and connections, to be such a dismemberment of the true frontals of the ruminant, as may be marked off with the pen on the upper surface of the skull!

The descending [rhinencephalic] plates of the prefrontal in the crocodile (fig. 9, 14) are subcompressed in the axis of the skull, and expanded laterally, especially at their upper part; where, in the alligator, I find them forming a shallow cup, concave forwards for the lodgment of the cartilaginous olfactory capsule,—of that part, namely, which is ossified in mammalia, and there developed into the great labyrinth of the superior turbinals and ethmoidal cells. The vertical plates, continued forwards from the prefrontals, which extend above to the nasal suture and descend into the vomerine groove below, to aid in forming the 'septum narium,' are cartilaginous in the crocodile: they are more or less ossified, and form the 'lamina perpendicularis ethmoidei' in mammals. The median plate, dividing the olfactory nerves at their exit, and developed backwards as a partial septum of the rhinencephalic chamber of the cranium, and continued into the simple interorbital septum of the crocodile, also remains cartilaginous: when ossified in mammals, it forms the 'crista galli.' Now not one of these cartilaginous representatives of the parts of the compound bone called 'ethmoid' in anthropotomy, is united or connected with the portions of the frontal in mammals which Cuvier has assumed to be the homologues of the prefrontals in the crocodile; those bones being in that reptile, as the prefrontals are in fishes, chiefly concerned in closing the anterior end of the cranial cavity, in giving exit to the olfactory nerves, in suspending the palatine arch, in connecting the vomer with the nasal vertically, and the nasal with the frontal and lacrymal horizontally, repeating in the crocodile for the latter purpose the development of the upper or horizontal plate which had almost or entirely disappeared in some of the intervening forms of reptiles. In most chelonians this portion of the prefrontal coalesces or is connate with the short nasal: but I have found the instructive exception presented by the existing freshwater tortoise (*Hydromedusa*) of the persistent suture between the nasals and prefrontals, repeated in two fossil chelonians (*Chelone planiceps* and *Chelone pulchriceps*)*.

Proceeding in the ascensive track of the homologies of the prefrontals, I have selected from the class of birds the skull of the ostrich (figs. 8 and 23), the representative of an aberrant order, in which every deviation from the type of the class that has been supposed to tend towards the *Mammalia*, tends equally or more towards the *Reptilia*†, and in which, conformably with the lower development of the respiratory system, the original sutures of the cranium, or in other words, the signs of the vertebrate archetype on which it is constructed, are longest retained. Were we to cut off the corresponding anterior angles of the frontals, no. 11, to those supposed to represent in mammals the bones we are in quest of, we should have even fewer of their characters than in the higher class alluded to, because the descending orbital plate is less developed, and the frontal, though its general size is much augmented, retains more of its oviparous horizontality as an expanded spine or roof-bone of the cranium.

There is a large bone (fig. 23, 73) bounding the anterior border of the orbit, and from which, as we have seen in the parrots, ossification sometimes extends backwards along the inferior contour of the orbit to the postfrontal. But this bone, besides its repetition of the connections of the lacrymal in the fish and crocodile, resting as in the latter animal upon the true malar bone, is either perforated or grooved by the lachrymal duct, which it defends in its course from the eye to the nose, and has none of the essential characteristics of the prefrontal. But we see on the exterior of the skull of the ostrich and other struthious birds‡, a distinct rhomboidal plate of bone interposed between the frontals and nasals, precisely in the situation in which the upper surface of the coalesced prefrontals appears in the skull of the frog and other anourous batrachians. In a nearly full-grown ostrich's skull, I removed the left frontal, nasal, lacrymal and tympanic bones, and the zygomatic arch, as in fig. 8, and found the facet in question to be the upper and posterior expanded surface of a large irregularly subquadrate compressed bone (*ib.* 14), consisting of two vertical compact plates coalesced at their periphery, and including a loose cancellous texture. The upper and posterior expanded surface of the bone extends a short way back beneath the frontals, descends and closes the anterior aperture of the cranium, and sends out from each side a plate of bone which arches over the olfactory nerves and forms the canals by which they are conducted along the upper part of the orbits. The anterior and upper surface of the bone again expands (at 14′, figs. 8 and 23), and there sustains, and is covered by, the nasal bones, and again overarches, and is sometimes perforated by the olfactory nerves (the course of which along the rhinencephalic continuation of the cranial cavity, is shown by the arrows, *cl.* 14, figs. 8 and 23) prior to their final expansion on the olfactory organ; the main body of the bone forms the fore-part of the interorbital septum and the back part of the nasal septum, a slight outstanding ridge or angle dividing the two surfaces: it rests below upon the rostral prolongation of the presphenoid, which, however, barely divides it from the semicylindrical grooved vomer (13) which sheathes the under part of that process. The posterior extremities of the palatines develope broad horizontal plates mesiad and upwards (fig. 23, 20), which join the lower border of no. 14, where it rests upon the presphenoid. The outer margins of the anterosuperior expansion of no. 14 come into contact with the lacrymals: the posterior border of the vertical or rhinencephalic plate joins and soon coalesces with the orbitosphenoids (10). Thus we have all the essential characters of the prefrontals in the fish, the frog and the crocodile, with a repetition of their first important modification in the tail-less batrachians, viz. that of median confluence; and it is not unimportant to observe that this is associated with the obliteration of other cranial sutures, by which also those batrachians resemble birds. The first step in the progress of this median approximation of the prefrontals, is the development of the plates which, in certain fishes, convert the olfactory grooves into foramina; these mesial plates next come into contact at the middle line, *e. g.* in *Xiphias* and *Ephippus*; they proceed to coalesce in the frog, and the prefrontals are so much further compressed in the bird that the olfactory grooves open upon the outer or lateral instead of the inner or mesial surfaces of the rhinencephalic plates: they are, however, very deep grooves in the ostrich. and in the apteryx are canals protected by a distinct external plate. The interruption of the direct vomerine connection by the prolonged presphenoid is the chief secondary modification of the prefrontals in the bird. No other bone in the bird's skull repeats the more essential characters of the prefrontals in fishes and reptiles, save the bone no. 14, figs. 8 and 23. Cuvier calls this bone the 'ethmoïde'; but blames the clear-sighted and consistent German anatomists who applied that name to the prefrontals in fishes and reptiles; yet the part of Cuvier's ethmoid in the bird answering to the 'lamina cribrosa' of the mammal, sometimes gives passage to the olfactory nerve by a single foramen, sometimes by merely a groove, a difference which does not prevent him adopting the homology here, though he opposes it to the adoption, by Bojanus, of the homology of the same part in the fish (*ante*, p. 215). The smooth plate forming, with the orbitosphenoid, the interorbital septum, is the 'os planum,' or papyraceous plate of the bird's ethmoid, with Cuvier: the masking of this part in most mammals by the downward development of the orbital plates of the frontal, offered no difficulty to the ethmoidal determination of no. 14 in the bird; and it forms as little valid objection to Oken's mode of expressing the ethmoidal homology of the prefrontals in the cold-blooded ovipara.

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* Report on British Fossil Reptiles, Trans. Brit. Assoc. 1841, pp. 169, 172.

† The urinary bladder and intromittent organ, *e. g.*: the modification of the feathers in the *Struthionidæ* is a degeneration of a peculiarly ornithic character; but not, therefore, an approximation to the hairy covering of mammals.

‡ In the emeu (*Dromaius ater*) at 14, fig. 1. pl. 39. Zool. Trans. t. iii.: and in the cassowary at *h*, fig. 3, taf. i. in Hallmann's 'Vergleichende Osteologie des Schläfenbeins.'

For the reasons before assigned, viz. that the terms 'frontal antérieur' had been given to the bone in question, no. 14, in those animals in which it deviates least from its general type, as the nasal neurapophysis, I retain the name 'prefrontal' for it under all its metamorphoses. Cuvier, after balancing the characters of the bones nos. 15, 22 and 73 (fig. 23) in birds, inclines to the opinion that 15 is the true nasal, and 22′ an essential part (nasal process) of the premaxillary: with regard to 73, he says, "les os externes et plus voisins de l'orbite seraient presque comme on le voudrait, ou des frontaux antérieurs ou des lacrymaux." In which case, no. 14 having been described as the 'ethmoid,' one or other of the above-named bones would be wholly absent in birds. "Ce que pourrait faire croire que c'est le frontal antérieur qui manque, c'est que dans les oiseaux il n'y a point de frontal postérieur, et que la paroi antérieur de l'orbite, à l'endroit ou le frontal antérieure se trouve ordinairement, est manifestement formée en grande partie par une lame transverse de l'ethmoïde[*]." But the postfrontal is not always absent in birds: it is present as a distinct bone, though small, in the emeu's skull, figured in the 'Memoir on the *Dinornis*' above-cited; and it is still more developed in that remarkable extinct (?) genus of wingless birds. Besides, to anticipate the subject of a subsequent chapter of this work, a parapophysis always disappears from a typical segment of the skeleton sooner than a neurapophysis. The rest of Cuvier's difficulty in the recognition of the prefrontal in birds was more nominal than real.

The ethmoid, in the restricted sense in which Cuvier applies the term in the crocodile and other animals with divided prefrontals, and in which I would apply it in those animals also in which the prefrontals have coalesced, is present but remains cartilaginous in the bird. In the mammal it becomes bony and contracts anchyloses not only with the still more reduced debris of the coalesced prefrontals, but also,—in consequence of the change of position of the prefrontals through the further progress of concentration, whereby they are drawn backwards closer to the prosencephalic part of the cranium, and in consequence of the concomitant expansion of the true frontals,—with the orbital plates of the frontals; and accordingly these plates usurp in most mammals the office and the position of the external parts of the prefrontals in the cold-blooded vertebrata[†].

The posterior part of the coalesced prefrontals (figs. 24 & 25, 14) divides the anterior aperture of the cranium into two outlets, upon the inner circumference of which the rhinencephala rest; each outlet being commonly closed by part of the olfactory capsules, which are ossified and perforated to receive the divisions of the olfactory nerves. When the prefrontals extend backwards and beyond the cribriform plates, they form what is termed the 'crista galli': this exists in comparatively few mammalia; but is as large in the seal tribe as in man. In the tapirs the prefrontals expand above and overarch the olfactory capsules, but their upper horizontal plates are overlapped by the nasals and true frontals. In the *Delphinidæ*, where the olfactory capsules are absent, the prefrontals expand posteriorly, and diverge from their median coalesced portions constituting the septum of the nasal passage, in order to form the posterior boundaries of those passages and the anterior wall of the cranial cavity. They again expand and form a thick irregular mass anterior to the nasal passages in some *Delphinidæ*, and in *Ziphius* ossification extends along the fibrous continuation of the prefrontals forwards to near the end of the premaxillaries[‡]. They are connate with the orbitosphenoids behind, and soon coalesce with the vomer below; they rise anterior to the frontals and support the stunted nasals which are wedged between the prefrontals and frontals. The cetacea are the only mammalia in which the prefrontals appear upon the exterior of the skull, and which in this respect resemble the reptilia.

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[*] Leçons d'Anat. Comp. 1837, t. ii. p. 508.

[†] Cuvier takes this ground in objecting to Oken's ethmoidal homology of the prefrontal in the crocodile, and says, "the ethmoid coexists in a cartilaginous state with, and is enveloped by, the prefrontal, 'comme la partie antérieure du frontal enveloppe l'ethmoïde des ruminans.'"—Hist. des Poissons, v. p. 235. The correspondence is exaggerated, but it matters not. There are other characters of the mammalian ethmoid, as the closing of the cranium anteriorly, the transmitting the olfactory nerves, &c., which are nowise manifested by Cuvier's cartilaginous 'ethmoïde' in the crocodile, and are very satisfactorily so by the prefrontals in that animal.

[‡] Ossem. Foss. v. pt. i. p. 351.

Cuvier describes the posterior and superior expanded and diverging plates of the prefrontals as "la lame cribreuse de l'ethmoïde:" the coalesced part forming the septum, he ascribes to the vomer[*]. Dr. Köstlin[†], also, who regards the ethmoid as no proper bone of the skull, but only an ossified organ of sense, yet describes, after the anthropotomists, the coalesced prefrontals as the cribriform and azygos processes of the ethmoid ('Siebplatte' and 'Scheidewand des Siebbeins,' pp. 85. 89) in cetacea which have no organ of smell. In a young balænoptera, in which the frontals, the vomer and the nasals were ossified, I find the prefrontals as two cartilaginous plates, extending from the nasals above to the groove of the vomer below. In the manatee the essential parts of the prefrontals which close the cranial cavity anteriorly, and give exit to the olfactory nerves, are thick and unusually expanded. But in no mammal do these parts, with their continuation, the 'lamina perpendicularis,' which, as the coalesced neurapophysial plates of prefrontals, brings the vomer below in connection with the nasals above, ever undergo such modifications as to obliterate their true and essential homological characters.

In proceeding next to consider the special homologies of the bones of the arch closed by the premaxillaries (22) and constituting the 'upper jaw,' I commence with the palatines (20), because they form, throughout the vertebrate series, the most constant medium of suspension of that arch to the anterior cranial segment formed by the vomer, prefrontals and nasal. This 'secret affinity,' as Goethe would have termed it, before the knowledge of the general type had revealed its nature, is manifested by the process of the palatine in man, which creeps up, as it were, into the orbit to effect its wonted union with the prefrontal, to that part of the bone, viz. of which Cuvier had recognised the homologue in his 'ethmoïde' of the bird[‡]. It is the very constancy, indeed, of these and other connections which has exempted the palatine from the different determinations and denominations attached to other bones, and which renders further discussion of its special homology unnecessary here.

Passing over, for the same reason, the maxillary (21) and premaxillary (22); and referring to the excellent treatise by Dr. Köstlin[§] for the grounds of the determination of the 'pterygoid' (24), I proceed to notice other bones which, diverging from the maxillary arch, serve to give it additional fixation and strength in the air-breathing vertebrates. The first of these is the malar bone (fig. 11, 26), the homology of which has been traced without difference of opinion throughout the mammalian class; where, however, the inconstancy of its proportions, number of connections, and very existence, is sufficient to indicate its comparative unimportance as an element of the maxillary arch. It is absent in many insectivores (*Centetes*, *Echinops*, *Sorex*): it has not been detected as a distinct bone in the zygomatic arch in the monotremes, on account perhaps of its early coalescence, as in birds, with the maxillary (fig. 12, 21, 26): in *Myrmecophaga gigantea* and *Manis*, it projects backwards, as a styliform appendage, from the maxillary, but does not attain the squamosal; whilst in the sloths and their extinct congeners the gigantic megatherioids, the malar presents its maximum of development and complexity[‖]. In the *Delphinidæ*, again, the malar is much reduced: its slightly expanded maxillary end forms part of the orbit and joins the frontal; the rest extending backwards, as a very slender style, beneath the orbit to the squamosal. The malar joins the post-orbital process of the frontal in the *Manatus senegalensis*, the hippopotamus, the solipeds, and ruminants, some carnivores and the lemurs; in the true quadrumanes and man it joins the alisphenoid, and sometimes also the parietal.

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[*] Ossem. Foss. v. pt. i. pl. xxvii. fig. 3, 4.

[†] Der Bau des Knöchernen Kopfes, p. 11.

[‡] See the passage above quoted from the 'Leçons d'Anat. Comp.' ii. p. 368.

[§] *Op. cit.* p. 323.

[‖] Description of the *Mylodon robustus*, 4to, p. 19.

The presence, form and connections of the malar are much more constant in the class of birds; where, however, it must be sought for as an independent bone at an early period. In the young ostrich (fig. 23, 26) it is reduced to the form of a simple, straight, slender style, and coalesces first with the similarly-shaped squamosal (27), and next with the malar process of the maxillary (21"). In the crocodile the malar bone (fig. 22, 26) becomes more developed, and adds the connections with the postfrontal (12) and the ectopterygoid (24') to the more constant ones with the maxillary (21) and squamosal (27), which alone sustain it in birds. In most of the chelonians the malar presents the same connections as in the crocodile, but is transmuted from a 'long' to a 'flat' bone. It retains the expanded shape in the agama; but in most other lizards it resumes the styloid form; being broadest, however, in those genera, *e. g. Iguana, Thorictes, Tejus*, in which it extends from the maxillary to the postfrontal and squamosal; in the *Varani* it projects freely backwards, like a styliform appendage of the maxillary, as in the toothless mammalian *Bruta*, above-cited.

There is no malar bone in ophidians and batrachians. The lower portion of the tympanic pedicle in the *Anoura* sends forward a process which joins a backward prolongation of the maxillary: in all other batrachia the lower portion of the tympanic pedicle is restricted to its normal connections and to its function of affording articulation to the lower jaw. With regard, therefore, to the zygomatic modification of this portion of the pedicle in anourous *Batrachia*, some may deem it the homologue of the malar; and, in marsupial quadrupeds, the malar actually forms part of the glenoid cavity for the lower jaw: or it may be regarded as the squamosal, which constantly supports the lower jaw in mammals: or it may be viewed as the coalesced homologue of both bones: or finally, as a simple modified dismemberment of the tympanic pedicle of the higher reptiles and birds; effecting a union with the maxillary bone which makes it analogous to, but not, therefore, homologous with, the distinct malar and squamosal in those higher vertebrates. This is a question of special homology on which I am unwilling at present to express a decided opinion: but viewing the inconstancy of the squamosal in reptilia, and its deprivation of the function of exclusively supporting the mandible in all ovipara, I am disinclined to adopt the idea of its sudden restitution to that mammalian function in frogs and fishes; yet, if either of the bones 26 and 27 are to be selected as the homologue of the hypotympanic (28d) of batrachians and fishes, I should regard the claims of the squamosal to be stronger than those of the malar, which Cuvier has chosen. The further subdivision, however, of the tympanic pedicle in fishes, prepares us, in the ascensive comparison, for the simple division of the pedicle in batrachia, and for recognising in the lower articular portion a vegetative dismemberment of 26 in the crocodile.

The characters and chief changes, in respect of connections and functions, of the squamosal (27) in the mammalia have already been noticed in the discussion of the homologies of other elements of the complex 'temporal bone' in that class. In birds the bone (fig. 23, 27) undergoes the same change of form which has been noticed in the jugal, viz. from the squamous to the styloid. It continues, however, to connect the malar with the tympanic as it does in figs. 11 and 12, but it has no connections with other bones. Cuvier having been led to recognise the squamosal in the mastoid (fig. 23, 8) of birds, does not distinguish 27 from 26, the true 'jugal:' and Geoffroy viewing the 'portion écailleuse' of the temporal in that cranial bone of the bird, which he figures under the letter R, fig. 17, pl. 27 (Annales du Muséum, x.), calls the true squamosal, the original separation of which from the malar he had noticed in the chick, 'jugal postérieure.' He did not admit that this division of the zygomatic style was constant or common in the osteogeny of the skull of birds: but I have always found such division in the embryo, and it continues longer than usual in those very species, *e. g.* the duck and ostrich (fig. 23, 26, 27), in which Geoffroy denies its existence (*l. c.*, p. 361). Oken accurately describes the two constituents of the zygoma in the skull of the goose, in his characteristic and original Essay*, where he calls the posterior piece (27) the humerus, and the anterior one (26) the radius of the head. Bojanus†, who also recognised the fact of the essential individuality of the bone (27) in birds, but who saw the homologue of the squamosal rather in the tympanic (28), calls it 'os zygomaticum posterius.' I could cite other testimonies to the primitive existence of the distinct bone in birds connecting the malar with the tympanic; but the fact which chiefly concerns us here is, that if the special homology of no. 8 with the mastoid, and that of no. 28 with the tympanic be proved, we then have a bone presenting the most constant connections of the squamosal in no. 27: if, however, that name be transferred, as has been done by Cuvier, Bojanus‡ and Geoffroy, to other bones, then a new bone and a new name must be introduced into vertebrate craniology, for which, as I trust I have shown, there is no sufficient ground.

Both Oken and Bojanus rightly discern in the permanently distinct bone which, in the crocodiles (fig. 22, 27) and chelonians, connects the malar (26) with the tympanic (28), the homologue of the bone they call 'cranial humerus,' or 'zygomaticum posterius' in the bird. Cuvier is more accurate in his determination of this bone (fig. 23, 27) as the 'squamosal' in reptiles; but again at the expense of his consistency in regard to the characters of his squamosal in the bird: for the homology of no. 8 (Cuvier's 'squamosal') in fig. 22 with no. 8 (Cuvier's 'mastoid') in fig. 23, is as obvious and unmistakeable as is that of no. 27 (Cuvier's 'squamosal') in fig. 22 with no. 27 (his dismemberment of the jugal) in fig. 23. The squamosal is relatively stronger in crocodiles than in birds, and in many chelonians resumes its flat, scale-like form; although, as Cuvier well observes, it answers, in function, only to the zygomatic part of the mammalian squamosal:—"c'est un temporal dont la partie crâniale a disparu§." In lizards the squamosal again resumes the zygomatic or styloid shape, connecting the mastoid and tympanic with the postfrontal, and usually also with the malar; the posterior connections being here, as in mammals, the more constant ones.

As the squamosal varies in form with the malar, so it likewise disappears with it in ophidians; unless the anatomist, tracing it descensively, prefers to see it again in the peculiarly developed hypotympanic of the anourans. According to this view of the sudden resumption of its mammalian function in regard to the lower jaw in batrachia, the name 'squamosal' may be transferred to the hypotympanic in fishes; and, if we must view the pedicle (28 *a—d*, fig. 5) as 'homologically compound,' and not, like the mandibular ramus, 'teleologically compound,' *and* seems to me a less arbitrary selection from the pieces of that long and subdivided pedicle, for the representative of the squamosal, than the proximal or uppermost piece (28a) to which Cuvier has applied that name. If, indeed, Bojanus could have determined to his own satisfaction or that of other anatomists, that the pedicle (28, fig. 23), articulated by one end to the mastoid, and by the other to the mandible, in birds, was the 'squamosum,' then there would have been some ground for regarding the bone (28a, fig. 5) connected in fishes, with the mastoid as the 'squamosum.'

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* Ueber die Bedeutung der Schädelknochen, 4to, 1807, p. 12.

† Anatome Testudinis Europææ, fol. Parergon, 1821, p. 178, fig. 196, *i*.

‡ The tympanic bone 28 is described in the same work as 'squamosum sive quadratum,' (fig. 196, *g*.): the mastoid is rightly named.

§ Ossemens Fossiles, 4to. t. v. pt. ii. p. 86.

But when Cuvier had persuaded himself that the bone no. 8, fig. 23, in birds, to which the tympanic pedicle is articulated, was the 'écaille du temporal,' we feel at a loss to know on what principles special homologies can be traced, when we find the name transferred to the upper part of the tympanic pedicle in fishes (fig. 5 28 a), which is articulated to the bone (8) unequivocally answering to Cuvier's 'écaille du temporal' in birds. M. Agassiz is more consistent, and abandons with reason the Cuvierian determination of the squamosal in fishes: if, however, the grounds assigned are conclusive as to the homology of no. 8, figs. 8 & 23 in birds with the mastoid of mammals and reptiles, M. Agassiz cannot be correct in regarding the bone no. 8, fig. 5 in the fish, as the 'écaille du temporal.'

With reference to the idea entertained by Spix, Geoffroy and Agassiz, of the homology of the suborbital muciferous scale-bones in fishes (pl. 1, fig. 1, 73) with the malar bones of higher vertebrates, I may refer to what has already been said in regard to the actual repetition of the osseous arch connecting the prefrontal with the postfrontal in certain birds (*ib.* fig. 1, 73), where that arch coexists with, and independently of, the bone (*ib.* 26) recognised as the 'malar' by both Spix and Geoffroy. The connection of the malar, even in mammals, with the lacrymal and post-frontal is less constant and characteristic of the bone than that with the maxillary and squamosal. And it may further be remarked, that the functional character of circumscribing a mucous duct, manifested by the lacrymal or anterior end of the upper zygomatic or suborbital arch in the parrot, is superadded to the character of connections in proof that such arch, and not the true zygomatic arch below, is homologous with the suborbital chain of bones in fishes. All these discrepancies as to the jugal and squamosal in fishes arise, in my opinion, out of the circumstance that those bones are normally absent in that class; both 26 and 27, figs. 11, 22, 23, 24, 25, being accessory parts, developed only in saurians, chelonians, birds and mammals, for additional fixation of the upper jaw, or for additional expansion of the cranium, or for both purposes*.

According to this view, I regard the tympanic (28) as essentially characterized in the oviparous vertebrates (fishes, reptiles, birds) by its free articulation by a convex condyle with the mastoid above, and by a convex condyle with the mandible below; and I regard its subdivisions in the lowest of these vertebrates, in the same light as the subdivisions of the mandible itself. The formation of the tympanic cavity and support of the tympanic membrane are secondary functions. The tympanic pedicle is essentially a single cranial element, and actually so in all air-breathing vertebrates above batrachians. We see plainly, even in the frog, that the portion which supports the 'membrana tympani' is a mere exogenous process of the pedicle: it has still less the appearance of a distinct part or process in the saurians, chelonians and birds: and when the tympanic is excluded by the squamosal in mammals from its normal office of supporting the mandible, it still manifests its character of

* The inconstant ossicle suspended to the back part of the free extremity of the maxillary in the percoid fishes would have the best claim to homology with the malar, if the further subdivision of the maxillary in the herring and lepidosteus did not indicate it to be a vegetative dismemberment of that bone.

unity, whether it be expanded into a 'bulla ossea,' extended into a long tube or meatus, or both, as in fig. 24, 28, or whether, as in fig. 25, it be reduced to a mere ring or hoop supporting the tympanic membrane, until it coalesces with other parts of the temporal, to form the tympanic or 'external auditory process' of that bone. In no air-breathing vertebrate have I ever found, or seen described, the separation of the part of the tympanic forming the wall of the tympanic chamber from the part supporting the tympanic membrane, or this distinct, save in batrachia, from the part supporting the lower jaw*. The tympanic pedicle is still further subdivided in fishes; but M. Agassiz's original idea of the 'epitympanic' as a dismemberment of the pedicle, which he proposed to call '*os carré supérieur*,' is, in my opinion, much more consistent with nature than his later determination of that bone as the 'mastoid,' or than Cuvier's attempts to find the homologues of both the mammalian 'squamosal' and 'jugal' in the piscine subdivisions of the same pedicle. There is as little ground for making the zygomatic process a distinct element from the squamous portion, as for severing the annular process from the rest of the tympanic. This idea of the zygomatic as an independent piece, which Dr. Köstlin has also adopted, seems to rest only on the mal-determination by Bojanus and Oken of the true squamosal in birds and reptiles as the 'zygomaticum' or 'jugale posterius': and the idea was perhaps further strengthened in the mind of M. Agassiz, by what he deems to be the essential and characteristic function of the squamosal. But its protective cerebral or cranial scale is a peculiarly mammalian development; much reduced in the ruminants and cetacea, and totally disappearing in the oviparous vertebrates. The zygomatic functions and connections are, notwithstanding a few exceptions, as in the scaly *manis* and a few lizards, the essential homological characters of the 'squamosal.' The necessity for forming an opinion of the essential nature and general homologies of the parts blended together in the human 'os temporis' by the ascensive or synthetic method, is strikingly exemplified by the results of the application of M. Agassiz's idea of its nature to his determination of the bones in the head of fishes.

As the palato-maxillary arch in most air-breathing vertebrates supports, according to my views, certain appendages, *e. g.* the malar and squamosal, which are not present in fishes; so, I believe, with Cuvier, that the tympano-mandibular arch supports in fishes, certain appendages, which are not developed in any other class. It is this fact, chiefly, that has led to so much discrepancy in the attempts to determine by reference to bones in higher vertebrates the opercular bones of fishes,—the chief battle-field of homological controversy. All the four opercular bones forming the diverging appendage of the tympano-mandibular arch (fig. 5, 34 to 37) were deemed by Cuvier to be peculiar ichthyic super-additions to the ordinary vertebrate skeleton; whilst by Spix, Geoffroy, and De Blainville they are held to be modifications of parts which exist in the ordinary or endo-skeleton of other vertebrata. The learned Professor of Comparative Anatomy in King's College, London, who regards this as "the more philosophical mode of considering them[*]," has briefly stated the homologies proposed by the supporters of this view, viz. that the opercular bones are gigantic representatives of the ossicles of the ear (Spix, Geoffroy, Dr. Grant[†]): or that they are dismemberments of the lower jaw (De Blainville, Bojanus),—a view refuted by the discovery of the complicated structure of the lower jaw in certain fishes, which likewise possess the opercular bones: he then cites a third view, viz. that they are parts of the dermal skeleton; "in short, scales modified in subserviency to the breathing function;" an opinion which Professor Jones frankly states that he derived from my Lectures on Comparative Anatomy, delivered at St. Bartholomew's Hospital in 1835, and which he adopts, although its accordance with his first proposition is not very clear. I have subsequently seen reason to modify that view, though it has received the sanction of the greatest ichthyologist of the present day, M. Agassiz; and, as I have since found, had presented itself so early as 1826, under a peculiar aspect to the philosophical mind of Professor Von Baer. In his admirable paper on the endo- and exo-skeleton, M. Von Baer expresses his opinion, that the opercular bones are (dermal) ribs or lateral portions of the external cincture of the head[‡]. The idea of the relationship of the opercular flaps to locomotive organs is presented by Carus, under the fanciful view of their homology with the wing-covers of beetles and the valves of a bivalve shell[§]. In 1836, M. Agassiz propounded his idea of the relation of the opercular bones to scales in a very precise and definite manner; though, as I have elsewhere shown[‖], the chief ground of his opinion is erroneous. He says, "Les pièces operculaires des poissons ne croissent pas, comme les os des vertèbres en général, par irradiation d'un ou de plusieurs points d'ossification; ce sont, au contraire, des véritables écailles, formées, comme celles qui recouvrent le tronc, de lames déposées successivement les unes sous les autres, et dont les bords sont souvent même dentelés comme ceux des écailles du corps. Tels sont l'opercule, le sub-opercule, et l'inter-opercule. Le supra-scapulaire même peut être envisagé comme la première écaille de la ligne latérale, dont le bord est également dentelé. On pourrait dire aussi que le scapulaire n'est qu'une très grande écaille de la partie antérieure des flancs*." And he adds, "L'opinion que j'ai émise à leur égard prouve que je suis loin d'admettre les rapports que l'on a cru trouver entre les pièces operculaires et les osselets de l'oreille interne†."

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* M. Agassiz applies the subjoined analysis of the 'temporal bone' to elucidate the homologies of the skull of fishes:—"Nous distinguons encore dans le *temporal complet* les parties suivantes: l'*écaille*, servant de complément à la paroi latérale du crâne dans sa partie postérieure; le *mastoïdien*, servant de rempart postérieur à la cavité tympanal; *la caisse*, logeant les parties principales de la cavité tympanale; *l'anneau tympanique*, servant d'appui à la membrane du tympan; l'*apophyse jugal*, formant l'appui postérieur de l'arcade zygomatique; l'*apophyse styloïde*, offrant une insertion à l'os hyoïde, par laquelle ce dernier se fixe au crâne; et enfin l'*os carré*, formant la surface articulaire sur laquelle la mâchoire inférieure exerce ses mouvemens. La manière variée dont ces différentes pièces se soudent ensemble, se séparent et se combinent, occasionnent ces innombrables variations auxquelles le temporal est sujet dans son ensemble. L'*écaille du temporal* est destinée, comme nous venons de le voir, à protéger les parties cérébrales postérieures de la tête, sur la face latérale du crane."—Recherches sur les Poissons Fossiles, t. ii. pt. 2, 1843, p. 62.

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[*] Professor Rymer Jones, General Outline of the Animal Kingdom, 8vo, 1841, p. 509.

[†] Lectures, Lancet, Jan. 11, 1834, p. 573; Outlines of Comp. Anat. p. 64.

[‡] "In mancher Beziehung gehören die Kiemendeckel zu ihr, und ich halte sie um so mehr für (Haut) Rippen, d. h. für Seitentheile der äussern Ringe des Kopfes, da ich sie auch in den gewohnlichen Knockenfischen für nichts anderes ansehen kann. Hat bei diesen auch der oberste Knochen des Kiemendeckels wenig Aehnlichkeit mit Rippen, so geht dagegen der unterste so unverkennbar in die strahlender Kiemenhaut über, das der Uebergang gar nicht zu verkennen ist."—Meckel's Archiv, 1826, 3 heft, p. 369.

An analogous idea of the relation of the opercular bones to the inferior or costal arches was proposed by Geoffroy St. Hilaire (see Annales des Sciences, t. iii. pl. 9, and Cuvier, Hist. des Poissons, i. p. 232), and has been adopted by the learned Professor of Comparative Anatomy in University College, who, speaking of the occipital vertebra, says, "The two external and the two lateral occipitals form the upper arch, and the two opercular and two subopercular bones constitute the lower arch." (Lectures, Lancet, 1834, p. 543.) He subsequently, however, adopts and illustrates (p. 573) the homology of the opercular bones with the 'ossicula auditûs' of mammalia; and in the 'Outlines of Comp. Anat.' cites only the Spixian and Blainvillian hypotheses (pp. 64, 65). In my Hunterian Lectures (vol. ii. 1836, pp. 113, 130), I have adduced the grounds which have led me to the conclusion that the opercular bones are neither ribs of the exo-skeleton, nor inferior arches of the endo-skeleton, but persistent radiating appendages of an inferior (hæmal) arch; not, however, of the occipital vertebra, but of the frontal; just as the branchiostegal rays are the appendages of the hæmal arch of the parietal, and the pectoral fins of that of the occipital vertebra. That parts of both endo- and exo-skeleton may combine to constitute the opercular fin is the more probable, inasmuch as we see the same combination of cartilaginous and dermal rays in the pectoral fins of the plagiostomes, and in the median fins of most fishes.

[§] Urtheilen des Knochen und Schalengerüstes, fol. p. 122.

[‖] Lectures on Vertebrata, p. 139.

I apprehend that the idea of the development of the opercular bones by the successive excretion or deposition of layers, one beneath the other, according to the mode in which M. Agassiz supposes scales to be formed, was derived merely from the appearance of the concentric lines on the opercular, subopercular, and interopercular bones in many fishes. I have examined the development of the opercular bone in young gold-fish and carp, and I find that it is effected in precisely the same manner as that of the frontal and parietal bones. The cells which regulate the intussusception and deposition of the earthy particles make their appearance in the primitive blastema in successive concentric layers, according to the same law which presides over the concentric arrangements of the radiated cells around the medullary canals in the bones of the higher vertebrata: and the term 'successive deposition,' in the sense of excretion, is inapplicable to the formation of the opercular bones. The argument in favour of their dermal character drawn from the phænomena of the development of the opercular flap, would equally apply to prove the bones (ulna, radius, carpus, &c.) supporting the pectoral fin, to be 'dermal' bones‡.

The interopercular as well as the preopercular bones exist in the *Lepidosiren annectens* with all the characters, even to the green colour, of the rest of the ossified parts of the endo-skeleton; the preopercular, as an appendage to the tympanic arch, retaining its primitive embryonal subcylindrical form, the interopercular being partly attached to the hyoid arch. Of the suprascapular there is no trace in the lepidosiren; but in the sturgeon it plainly exists as part of the cartilaginous endo-skeleton, under the same bifurcate form, and double connection with the cartilaginous skull, which it presents in most osseous fishes. The large triangular bony dermal scale firmly adheres to its broad, triangular, flat, outer surface. The epi- and meso-tympanic cartilages in like manner expand posteriorly, and give a similar support to the large opercular ganoid scale. Were the supporting cartilages of the opercular and suprascapular scales to become ossified in the sturgeon, they might become anchylosed to the dermal bony plates, and bones, truly homologous with the opercular and suprascapular in ordinary osseous fishes, would thus be composed of parts of the endo- and exo-skeleton blended together. I cannot, therefore, concur with Von Baer in the opinion that the opercular bones are ribs of the exo-skeleton, nor with Agassiz that both the opercular and suprascapular bones are merely modified scales. In explaining my views of the opercular bones, I am compelled, believing them to have no special homologues in higher animals, to express those views in the terms of a higher generalization. The suprascapular bone (fig. 5, 50) is the upper or first part of the hæmal arch of the occipital segment of the skull, and corresponds in serial homology with the epi-tympanic portion (28 *a*) of the mandibular arch, and with the palatine portion (20) of the maxillary arch. The opercular bones are the diverging appendages of the tympano-mandibular

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* Recherches sur les Poissons Fossiles, livraison 6me, 1836, tom. iv. p. 69.

† *Ib.* p. 73.

‡ "L'embryologie nous prouve, en effet, que la formation de l'appareil operculaire n'est qu'un simple produit de la peau, qui peu-à-peu s'étend par dessus les branchies, d'abord entièrement dégagées dans l'embryon."—*Ib.* p. 64.

arch, and correspond, in serial homology, with the branchiostegal appendages of the hyoid and the pectoral appendages of the scapular arches, and have the same title to be regarded as cephalic fins, and as parts of the normal system of the vertebrate endo-skeleton; but neither opercular bones nor branchiostegal rays are retained in the skeletons of higher vertebrata. All diverging appendages of vertebral segments make their first appearance in the vertebrate series as 'rays'; and the opercular bones are actually represented by cartilaginous rays, retaining their primitive form in the plagiostomes. In the conger the subopercular still presents the form of a long and slender fin-ray.

The opercular and subopercular, in ordinary osseous fishes, may frequently coalesce, like the suprascapular, with their representative scales of the dermal system; but they are essentially something more than peculiarly developed representatives of those scales. M. Agassiz, indeed, excepts the preopercular bone from the category of "pièces cutanées," believing it to be the homologue of the styloid process of the temporal bone in anthropotomy, or the 'stylo-hyal' of vertebrate anatomy, as the piece, viz. which completes the hyoid arch above. "C'est en effet," he says, "cet os à la face interne duquel l'os hyoide des poissons est suspendu, qui s'articule en haut avec le mastoïdien et très souvent même sur l'écaille du temporal." So far as my observation has gone, it is a rare exception to find the hyoid arch suspended to the preoperculum; the rule in osseous fishes is to find the upper styliform piece of the hyoid arch (fig. 5, 38) attached to the epi-tympanic (28 *a*) close to its junction with the meso-tympanic bone (28 *b*). It is equally the rule to find the preopercular (34) articulated with the epi-, meso-, and hypo-tympanics; and it is an exception, when it rises so high as to be connected with the mastoid ('écaille du temporal' of Agassiz). If the stylo-hyal be not the upper piece of the hyoid arch displaced, and if the upper piece connecting that arch with the mastoid is to be sought for in osseous fishes, I should rather view it in the posterior half of the epi-tympanic (28 *a*), which is usually bifurcate below and very commonly also above, when the posterior upper division articulates with the mastoid, and one of the lower divisions with the hyoid arch.

The normal position, form, and connections of the preoperculum clearly bespeak it to be the first or proximal segment of the radiated appendage of the tympano-mandibular arch: the opercular, subopercular, and interopercular bones form the distal segment of the same appendage.

M. Vogt, in supporting M. Agassiz's views of the Ganoid order, reiterates his original idea that the preopercular bone is the proximal piece (styloid) of an arch distinct from the tympano-mandibular one; but as the chief ground of this opinion rests on a simple question of fact easily determinable, viz. whether, as a rule, the hyoid arch is suspended from the preoperculum, and this from the mastoid in fishes, neither of which accord with my observation of their connections of those parts, the verdict may be left to the experience of other observers. From a remark of M. Vogt's*, viz. that "M. Müller attache, à ce qu'il parait, trop peu d'importance *à ce fait*, que toujours le préopercule, et cela aussi chez les Siluroïdes, sert de point d'attache à l'arc hyoïdien," it would seem that, perhaps, the accomplished physiologist and ichthyologist of Berlin had not found *the fact*; and, therefore, gave not more than its due importance to the rare exceptional circumstance of such an attachment. The preopercular can be removed in most fishes, except where, as in the siluroids, it coalesces with the tympanic arch, without dislocating or disturbing the connections of the true stylo-hyal (fig. 5, 38) with the epitympanic (28*a*) from which it is normally suspended.

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* Annales des Sciences, 1845, p. 56.

M. Vogt correctly observes that the 'temporal' (epitympanic, 28 *a*), 'symplectique' (mesotympanic, 28 *b*), and 'jugulaire' (hypotympanic, 28 *d*), "à eux seuls forment déjà un arc suspensoir complet, à la face postérieure duquel le préopercule est seulement accolé*." But this only proves that the preoperculum is an appendage to such arch, not that it is a suspensory pier of a second arch.

The only essential modification which the siluroids present is the confluence of the preoperculum with the true tympanic pedicle, here reduced to a single piece. But this does not disprove its character as an appendage of the tympano-mandibular arch, any more than does the confluence of the ulna and radius with the scapular arch in the sturgeon disprove the character of those elements as appendages of that arch. I have not been able to trace in the siluroids the primitive boundaries of the coalesced preoperculum to such an extent as to justify the statement, that it is intercalated between the epitympanic and hypotympanic, replacing the mesotympanic: but, if the preopercular should extend in any siluroid fish so far as M. Vogt describes, this exceptional development would rather prove it to belong essentially to the tympanic and not to the hyoidean arch: at least it is only through this abnormal encroachment that the preopercular can detach the stylohyal from the epitympanic.

As the otosteals, or 'ossicula auditûs,' have borne a prominent share in the discussions of the special homologies of the tympanic pedicle and its appendages, I may here remark that the extension in the embryo mammal of the long and slender process of the malleus in the direction of the mandible, and its continuation or connection with the cylindrical cartilage (hæmal portion of the tympano-mandibular arch) from which the lower jaw is subsequently developed, is a circumstance which renders the idea of the malleus, at least, being a modified element of the tympano-mandibular arch in batrachians and fishes, worthy of consideration. The prolongation from the mesotympanic of the cylindrical cartilage, described by Meckel, and around which the mandible is ossified in fishes, and the characteristic cylindrical or styloid form of the mesotympanic, have induced M. Vogt† to view that bone, the 'symplectique' of Cuvier, as the homologue of at least part of the malleus; and at the same time of the bone called 'tympano-malléal' by Dugès (my 'hypotympanic') in the batrachians. M. Vogt offers no other reasons for the determination. I find that the cartilage which in the batrachians forms the medium of communication between the semi-ellipsoid ossicle (stapes) closing the fenestra ovalis and the tympanic membrane, is repeated or reproduced in the more malleiform cartilage connecting the columelliform stapes of the saurian reptiles to the membrana tympani. In birds a portion of the cartilage attached to the tympanum becomes ossified and coalesces with the columelliform stapes; and at the angle of union one or two cartilaginous processes exist, which some anatomists have compared with the incus. But all anatomists have concurred in recognising the homology of the peripheral bent-down portion of the long columella, which adheres to the membrana tympani, with the part of the malleus called 'manubrium,' or handle, in mammalia. The superadded modifications characteristic of the otosteals in this class, have their seat between the manubrium mallei and the stapes, and chiefly result in the development of the new bone called 'incus' and its epiphysis, which has been termed the 'os orbiculare.' Notwithstanding, therefore, the connection of the 'processus gracilis mallei' with the embryonic hæmal or visceral cartilage of the mandibular arch in mammals, the homology of the malleus is so clearly traceable down to its first independent manifestation in coexistence with the tympanic membrane of the batrachia, to which it connects the unequivocally acoustic ossicle representing the 'stapes,' that the reference of all the additional ossicular mechanism of the ear-drum to the same system of the skeleton as the petrosal itself, appears to me to be most consonant with the recognised facts in their development and comparative anatomy.

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* Annales des Sciences, 1845, p. 55.

† *Loc. cit.* p. 58.

M. Agassiz has never countenanced the idea of the reproduction of the mammalian tympanic ossicles in a magnified form in either the tympanic arch or its opercular appendages. Returning to the consideration of these bones in the last volume (p. 68) of his admirable 'Recherches,' he reaffirms his opinion, that the opercular, subopercular, and interopercular are 'osselets particuliers de la peau;' but calls them 'branchiostegal rays.' If he had meant that they were parts essentially distinct, but comparable to the true branchiostegals, he would have accurately enunciated their 'serial homology.' M. Agassiz, however, expressly repudiates this idea of representative relation, and affirms them to be part of one and the same series of rays. "Mais en disant que les pièces operculaires sont des rayons branchiostègues, je n'entends point faire une simple comparaison, mais bien affirmer, que je considère ces plaques osseuses simplement comme les rayons branchiostègues supérieurs*." This idea is, in fact, a necessary consequence of M. Vogt's conclusion, that the preoperculum is the upper or styloid element of the hyoidean arch. The combination of the opercular rays or bones with the branchiostegals in the support and movements of the continuous gill-cover and gill-membrane, does not prove them to be diverging appendages of the same arch, any more than the similar combination of the rays of the pectoral and ventral fins in the sucker of the *Cyclopterus* proves those rays to be parts of the same arch. And I may repeat that, admitting the humerus to be, as Bakker surmised, confluent in all fishes with the bone *52*, fig. *5*; and since in the plagiostomes, sturgeons and lophioids, the second segment of the rudimental fore-limb is not liberated from the supporting arch; so, likewise, the proximal member of the opercular limb may remain, or become in some instances confluent with its sustaining arch, without that exceptional state invalidating the determination deduced from its more constant and regular character as the proximal element of the free appendage to that arch.

Hyoid Bones.—The third inverted arch of the skull is suspended in fishes by a slender styliform bone, the 'stylohyal' (fig. *5*, 38), from the lower end of the epitympanic (28 *a*) close to the joint of the styliform 'mesotympanic' (28 *b*); and it is connected, through the medium of the posterior division and joint of the epitympanic, with the mastoid (8). Now, either that division of the epitympanic may be viewed, by virtue of its proper articular condyle above, and its connection with a distinct inverted arch below, as the proximal piece of that arch, coalesced with the proximal piece of the next arch in advance, which articulates with the post-frontal; or, it may be viewed as an excessive development of the proximal piece of the tympano-mandibular arch, which, extending backwards, has displaced the hyoid from the mastoid, just as the squamosal, by a similar backward development, in mammals, displaces the mandibular arch from the tympanic.

According to the first view, the bone no. 38 would be a dismemberment of the proximal element of the hyoid arch; according to the second view, it would be the entire element reduced and displaced: in both cases it would be homologous with the proximal slender piece of the hyoid arch in all

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* Recherches sur les Poissons Fossiles, v. pt. ii. p. 68.

vertebrata, and to which piece the term 'styloid' or 'stiliform' has been given from the fish up to man (see TABLE I.). The homology, indeed, is so obvious, that M. Agassiz, in accepting the conclusion of M. Vogt, that the bone (fig. 5, 34), peculiar to osseous fishes, which so rarely articulates directly with the mastoid or with the hyoid arch, and so constantly sustains the distal segment of the operculum, was the homologue of the 'processus stiliformis ossis temporis,' nevertheless retains the name 'styloïde' for the part no. 38 in question.

The true homology of no. 34, already explained, removes the anomaly of viewing that peculiarly piscine bone as the homologue of a constant element of the hyoid arch in all the vertebrate classes, and the greater anomaly of the introduction of a new element—a styloid piece of the os hyoïdes—in addition to the 'styloid process of the temporal' in fishes. The 'stylohyal' articulates below to the apex of a triangular piece (39), which is pretty constant in fishes, and to which I give the name of 'epihyal,' as being the upper of the two principal parts of the cornu or arch: the third longer and stronger piece is the 'ceratohyal' (*ib.* 40).

The keystone or body of the inverted hyoid arch is formed by two small subcubical bones on each side, the 'basihyals' (*ib.* 41). These complete the bony arch in some fishes: in most others there is a median styliform ossicle, extended forwards from the basi-hyal symphysis into the substance of the tongue, called the 'glossohyal' (*ib.* 42), or 'os linguale'; and another symmetrical, but usually triangular, flattened bone, which expands vertically as it extends backwards, in the middle line, from the basihyals; this is the 'urohyal' (*ib.* 43). It is connected with the symphysis of the coracoids, which closes below the fourth of the cranial inverted arches, and it thus forms the isthmus which separates below the two branchial apertures. In the conger the hyoidean arch is simplified by the persistent ligamentous state of the stylohyal, and by the confluence of the basi-hyals with the ceratohyals: a long glossohyal is articulated to the upper part of the ligamentous symphysis, and a long compressed urohyal to the under part of the same junction of the hyoid arch. The glossohyal is wanting in the *Muraenophis*.

The appendages of the hyoidean arch in fishes retain the form of simple, elongated, slender, slightly curved rays, articulated to depressions in the outer and posterior margins of the epi- and cerato-hyals: they are called "branchiostegals," or gill-cover rays, because they support the membrane which closes externally the branchial chamber. The number of these rays varies, and their presence is not constant even in the bony fishes: there are but three broad and flat rays in the carp; whilst the clupeoid *Elops* has more than thirty rays in each gill-cover: the most common number is seven, as in the cod (fig. 30, 44). They are of enormous length in the angler, and serve to support the membrane which is developed to form a great receptacle on each side of the head of that singular fish.

In the class of fishes, certain bony arches, which appertain to the system of the visceral skeleton, succeed the hyoidean arch, with the keystone of which they are more or less closely connected. Six of these arches are primarily developed, and five usually retained; the first four of these support the gills, the fifth is beset with teeth and guards the opening of the gullet: this latter is termed the 'pharyngeal arch,' the rest the 'branchial arches.'

The lower extremities of these arches adhere to the sides of a median chain of ossicles, which is continued from the posterior angle of the basihyal, or from above the urohyal, when this is ossified: the bones which form these extremities are the 'hypobranchials'; and they support longer bent pieces, called 'ceratobranchials.' It is with these elements of the branchial arches in fishes and perennibranchiate batrachians that we are chiefly concerned in tracing the homology of the hyoid apparatus in the air-breathing vertebrates. With regard to the branchial and pharyngeal arches, which attain their full development only in the class of fishes, I regard them as appertaining to the system of the splanchno-skeleton, or to that category of bones to which the heart-bone of the ruminants and the hard jaw-like pieces supporting the teeth of the stomach of the lobster belong. The branchial arches are sometimes cartilaginous when the true endoskeleton is ossified: they are never ossified in the perennibranchiate batrachians, and are the first to disappear in the larvæ of the caducibranchiate species; and both their place and mode of attachment to the skull demonstrate that they have no essential homological relation to its endoskeletal segments.

The hyoid arch or apparatus retains most resemblance to that of fishes in the *Siren lacertina*; the basihyal is simplified into a single osseous spatulate piece, with the bowl of the spoon anterior, and supporting a broad and flat semicircular glossohyal. A strong and thick ceratohyal is articulated by means of a small cartilage to the side of the expanded part of the basihyal, and a cartilaginous epihyal arches backwards from its upper end. A cartilaginous urohyal extends from the hind end of the basihyal, and expands into a radiated disc, which supports the membranous trachea and the simple glottis. One pair of bony 'hypobranchials' is articulated to the basi-uro-hyal joint and a second pair to the sides of the urohyal: and to the upper and outer ends of these are attached four pairs of cartilaginous 'ceratobranchials.' The fimbriated branchiæ are attached to the three anterior ceratobranchials.

In the proteus the urohyal is absent, and it is not again developed in any batrachian. The long subcylindrical basihyal supports a subcircular cartilaginous discoid glossohyal, and at the angle of union the bony ceratohyals are sent off. A pair of hypobranchials diverge from the end of the basihyal; to which a second small pair of basibranchials are loosely connected by an aponeurosis. These support three ceratobranchials on each side, which are bony.

In the newts there is neither a glossohyal nor urohyal, or but a rudiment of the latter, to each side of which are articulated two hypobranchials, whose distal ends converge on each side to support a single cartilaginous gill-less rudiment of a ceratobranchial. The special homologies of all those parts of the complex hyoid, rendered more complex by the retention of part of the branchial skeleton, are clearly demonstrated by pursuing the metamorphoses of the hyo-branchial skeleton in the larvæ of the anourous batrachians. In the full-gilled tadpole a short and simple basihyal supports laterally two thick and strong ceratohyals, and posteriorly two short and broad hypobranchials, to which four ceratobranchials are attached: all the parts are cartilaginous. The type of this stage is retained in the siren, with the histological progress to bone in the hyoid and hypobranchial pieces. The second well-marked stage in the tadpole shows an extension of the external and posterior angles of the hypobranchials, with progressive absorption of the cartilaginous ceratobranchials. The growth and divergence of the posterior angles of the hypobranchials refer to the development of the larynx, now commencing, which part they are destined to support. That period may be described as the third stage at which the ceratobranchials have disappeared, and the posterior angles of the hypobranchials increase in length and assume the character of posterior cornua of the os hyoides. The last and adult stage shows the ossification of the elongated angles of the hypobranchials, the coalescence of their cartilaginous bases with the basihyal, the expansion of the basihyal and extension of its anterior and external angles; in front of which the now long and slender ceratohyals usually coalesce with the basihyal; their opposite ends having shifted their attachments and retrograded, like other hæmal arches of the skull, in the course of the metamorphosis. In the case of the hyoid arch of the frog, the change of place is from the tympanic pedicle backwards to the persistent cartilaginous petrosal: and this is a very suggestive and significant change. All the parts of the hyoid remain cartilaginous except the appended and persistent detachments from the visceral system of the branchial arches: these long 'hypobranchials' ('cornes thyroïdiennes' of Cuvier and Dugés) diverge and include the larynx in their fork. The relative position, connexions and office in subserviency to the larynx, to which the retained parts of the splanchno-branchial arches are introduced in the lowest of the air-breathing vertebrates, are preserved in all the higher classes. The 'hypobranchials' are as constant in their existence, therefore, as the upper larynx itself, and attach themselves more especially to the thyroid element of that larynx. We recognise them by this relation in birds and man (46, figs. 23 and 25), where they always much exceed the parts of the true hyoid arch (cerato- and epi-hyals) in length; and in birds, where these elements (40, fig. 23) are sometimes obsolete and always rudimental, the hypobranchials have been mistaken by both Cuvier and Geoffroy* for the ceratohyals or anterior cornua.

For the modifications and special homologies of the complex hyoid apparatus in lizards, I refer to my 'Lectures on the Vertebrata.' The crocodiles offer a well-marked ordinal difference from those inferior sauria in this as in most other parts of their structure. The basihyal and thyrohyals have coalesced to form a broad cartilaginous plate, the anterior border rising like a valve to close the fauces, and the posterior angles extending beyond and sustaining the thyroid and other parts of the larynx. A long bony 'ceratohyal' (fig. 22, 40), and a commonly cartilaginous 'epihyal' (*ib.* 39), are suspended by a ligamentous 'stylohyal' to the paroccipital process; the whole arch having, like the mandibular one, retrograded from the connection it presents in fishes.

In birds as in cheionians, the ceratohyals are much reduced, and the chief 'cornua' of the hyoid are represented by the hypo- and epi-branchials (thyrohyals), which here attain their maximum of length and tenuity. The basihyal (fig. 23, 41), as in *Chelys*, is long and slender, but is always a simple piece; and, as in lizards, is usually most expanded posteriorly, from which expansion the thyrohyals (46) are sent off. Conforming with the long and slender tongue in most birds, the basihyal extends forwards, and is articulated with the rudimental ceratohyals (40), when these exist, at some distance from the thyrohyals. A commonly long and slender, sometimes spatulate glossohyal (42), is articulated to the fore-part of the basihyal; and a constantly long, slender and pointed urohyal (43) is articulated with the posterior end of the basihyal, and extends backwards beneath the trachea. The thyrohyals (46) diverge and include the larynx in their fork; and support at their extremities a bony or gristly (ceratobranchial) style (47). This is never attached by ligament to the base of the skull, but is suspended freely, as in the chelonia, by the glossohyoid and omohyoid muscles; it, however, curves over the back and upper part of the cranium in the woodpeckers, and the extremities of both cerato-branchials are inserted, by way of rare exception in that bird, into the right nostril.

In mammals the normal completion of the hyoidean arch, as it first appears in fishes, is again resumed, and that not by a slender cartilage, as in the frog, but by a chain of bones, in which we again recognise the cerato- (fig. 24, 40), epi- (39) and stylo- (38) hyals suspending the basihyal (41) and the tongue to the base of the skull, often to the petrosal, sometimes to the tympanic, or to the mastoid, or to the exoccipital. The ungulates and the true carnivora best display this type.

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* Dugés appears to have first pointed out this error, but without, however, perceiving the true homology of his 'cornes thyroïdiennes' with the hypobranchials of fishes.

In man (fig. 25) the ceratohyals are reduced, as in birds, to mere tubercles of bone (40), and the extent of the arch between them and the stylohyals, which become anchylosed to the temporal bones, retains its primitive ligamentous condition. Occasionally, however, ossification extends along the stylohyoid ligament, and marks out, as in the specimen figured by Geoffroy St. Hilaire (Philosophie Anatomique, pl. 4, fig. 87), the more normal proportions of the ceratohyal, and also the epihyal. Other examples of this 'monstrosity' are recorded in works on anthropotomy. The thyrohyal (46)—the last remnant of the branchial arches—maintains more constancy in its existence and proportions; but manifests its true character of free suspension below the skull, and an articulation by short ligaments to the angles or horns of the thyroid cartilage.

The remarks already made on the special homologies of the parts of the scapular arch and its appendages, preclude the necessity of further extending the present chapter of this work.

Chapter II.—General Homology.

Historical Introduction.

On taking a retrospect of the results of the researches of anatomists into the special homologies of the cranial bones, the student of the science, how little soever practised in such inquiries, cannot but be struck with the amount of concordance in those results. It must surely appear a most remarkable circumstance to one acquainted only with the osteology of the human frame, that so many bones should be, by the common consent of comparative anatomists, determinable in the skull of every animal down to the lowest osseous fish. This fact alone, so significant of the unity of plan pervading the vertebrate structure, has afforded me, at least, a large ground of hope and much encouragement to perseverance in the reconsideration of those points on which a difference of opinion has prevailed; and in the re-investigation of what is truly constant and essential in characters determinative of special homologies.

In this, as in every other inquiry into nature, the first labours are necessarily more or less tentative and approximative: but if errors have to be eliminated in the course of successive applications of fresh minds to the task, truths become confirmed and established. And I regard the body of such truths (see Table I.) to be now so great, in respect of the determination of the homologous bones in the heads of all vertebrate animals, as to imperatively press upon the thinking mind the consideration of the more general condition upon which the existence of relations of special homology depends.

Upon this point the anatomical world is at present divided, lacking the required demonstration. The majority of existing authors on comparative anatomy have tacitly abandoned*, or with Cuvier and M. Agassiz, have directly opposed the idea of 'special homology' being included in a higher law of uniformity of type.

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* Wagner, 'Lehrbuch der Zootomie,' 8vo, 1843, 1844. Siebold and Stannius, 'Lehrbuch der Vergleichende Anatomie,' 8vo, 1845, 1846. Milne-Edwards, 'Elemens de Zoologie,' 8vo, 1834. Prof. Rymer Jones, 'Outline of the Animal Kingdom and Manual of Comparative Anatomy,' 8vo. 1841. The sentiments which this pleasing and instructive writer expresses, are probably akin to those which have influenced the above-cited authors

Yet the attempt to explain, by the Cuvierian principles, the facts of special homology on the hypothesis of the subserviency of the parts so determined to similar ends in different animals,—to say that the same or answerable bones occur in them because they have to perform similar functions—involve many difficulties, and are opposed by numerous phænomena. We may admit that the multiplied points of ossification in the skull of the human fœtus facilitate, and were designed to facilitate, childbirth; yet something more than such a final purpose lies beneath the fact, that most of those osseous centres represent permanently distinct bones in the cold-blooded vertebrates. The cranium of the bird, which is composed in the adult of a single bone, is ossified from the same number of points as in the human embryo, without the possibility of a similar purpose being subserved thereby, in the extrication of the chick from the fractured egg-shell. The composite structure is repeated in the minute and prematurely-born embryo of the marsupial quadrupeds. Moreover, in the bird and marsupial, as in the human subject, the different points of ossification have the same relative position and plan of arrangement as in the skull of the young crocodile, in which, as in most other reptiles and in most fishes, the bones so commencing maintain throughout life their primitive distinctness. These and a hundred such facts force upon the contemplative anatomist the inadequacy of the teleological hypothesis to account for the acknowledged concordances expressed in this work by the term 'special homology.' If, therefore, the attempt to explain them as the results of a similarity of the functions to be performed by such homologous parts entirely fails to satisfy the conditions of the problem; and if, nevertheless, we are, with Cuvier, to reject the idea of their being manifestations of some higher type of organic conformity on which it has pleased the divine Architect to build up certain of his diversified living works, there then remains only the alternative that special homologies are matters of chance.

This conclusion, I apprehend, will be entertained by no reasonable mind; and reverting, therefore, to the more probable hypothesis of the dependence of the special resemblances upon a more general law of conformity, we have next to inquire, what is the vertebrate archetype? The gifted and deep-thinking naturalist, OKEN, obtained the first clew to this discovery by

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on this subject. "It is not by any means our intention to engage our readers in discussing all the conflicting and, sometimes, visionary opinions entertained by different authors relative to the exact homology of the individual bones forming this part of the skeleton; and we shall, therefore, content ourselves by placing before them, divested as far as possible of superfluous argumentation, Cuvier's masterly analysis of the labours of the principal inquiries concerning this intricate part of anatomy."—p. 494. A later English author, who has embodied a most valuable amount of careful and exact osteological observation in the article "Zoology" of the 'Encyclopædia Metropolitana' (4to, 1845), seems scarcely to regard even the determination of special homologies as a necessary object of anatomical research. Thus, in discussing the differences of opinion respecting the coracoid (fig. 5, 45). he says, "Bakker's view, however, if it be absolutely necessary to hunt up analogies, seems more correct."—p. 302.

This reserve is, however, perhaps less obstructive to the philosophical progress of anatomy and to the requisite resumption of original inquiry to that end, than the mere reproduction of the transcendental views of others without criticism or attempt to explain or refute the objections to such views which have been promulgated by so great authorities as Cuvier and Agassiz. Thus Bojanus's 4-vertebral theory of the cranial part of the skull is adopted by M. De Blainville (Ostéographie, 4to); whilst Dr. Grant (Outlines of Comparative Anatomy, 8vo, 1835, p. 63) deems the composition of the skull, in fishes, to correspond nearly with Geoffroy's theory of this part of the skeleton being composed of seven vertebræ, each consisting of a body with four elements above and four elements below.

the idea of the arrangement of the cranial bones of the skull into segments, like the vertebræ of the trunk. He informs us that walking one day in the Hartz forest, he stumbled upon the blanched skull of a deer, picked up the partially dislocated bones, and contemplating them for a while, the truth flashed across his mind, and he exclaimed "It is a vertebral column!*" Oken afterwards tested and matured this happy inspiration by examining the skulls of a cetacean, a chelonian, and a cod-fish in Dr. Albers's museum at Bremen; and on his return to Jena in 1807, he published his beautiful generalization in a now very scarce Introductory Lecture, or "Programm beim Antritt der Professur," entitled 'On the signification of the bones of the skull'†. He illustrates his views by reference to the skull of a ruminant. "Take," he says, "a young sheep's skull, separate from it the bones of the orbit, also those cranial bones which take no share in the formation of the 'basis cranii,' *e.g.* the frontal, parietal, ethmoid and temporal, and there will remain an osseous column which any anatomist, at first glance, would recognise as three bodies of a kind of vertebræ with transverse processes and foramina. Replace the cranial bones with the exception of the temporals, for, without these, the cavity is still closed, and you have a cranial vertebral column, which differs from the true one ('von der wahren') only by its more expanded neural canal (Ruckenmarkshöhle). As the brain is a more voluminously developed spinal chord, so is the brain-case a more voluminous spinal column. As the cranium includes, then, three vertebral bodies, so must it have as many vertebral arches. These are next to be sought out and determined. One sees the sphenoid divided into two vertebræ; through the foremost pass the optic nerves, through the hindmost the maxillary nerves (*par trigeminum*). I call one the 'eye-vertebra' (Augwirbel), the other the 'jaw-vertebra' (Kieferwirbel). Upon this latter abuts the basilar process of the occipital bone and the petrous bones: both belong to one whole. As the optic nerve perforates the 'eye-vertebra,' and the trigeminus the 'jaw-vertebra,' so the acoustic nerve takes possession of the hindmost vertebra. I call it, therefore, 'ear-vertebra' (Ohrwirbel): and I regard this as the first cranial vertebra; the jaw-vertebra as the second, and the eye-vertebra as the third."—*ib.* p. 6.

After entering upon the difficulties which beset him in determining whether the petrosal belonged to the first (Ohrwirbel) or the second (Kieferwirbel), and enunciating his views on the essential relations of each cranial vertebra with a single special sense (excluding, however, smell and taste, as being inferior in dignity to the others), Oken proceeds, in his characteristic bold metaphorical language:—"Bones are the earthy hardened nervous system: Nerves are the spiritual soft osseous system—Continens et contentum."

"Between the sphenoid and occipital, between the sphenoid and petrosal, between the parietal (the temporal being removed) and the occipital, there runs a line which defines the anterior boundary of the first vertebra. In the line between the two sphenoids, or that which in man extends anterior to the pterygoid processes laterally and upwards through the fissura orbitalis superior, anterior to the great ala, and finally between the frontal and the parietal bones, we trace another line, which divides the second from the third vertebra" (*ib.* p. 7).

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* "Im August 1806 machte ich eine Reise über den Hartz,"—"ich rutschte an der Südseite durch den Wald herunter—und siehe da; es lag der schönste gebleichte Schädel einer Hirschkuh vor meinen Füssen. Aufgehoben, umgekehrt, angesehen, und es war geschehen. *Es ist eine Wirbelsäule*! fuhr es mir wie ein Blitz durch Mark und Bein—und seit dieser Zeit ist der Schädel eine Wirbelsäule."—Isis, 1818, p. 511.

† Uber die Bedeutung der Schädelknochen, 4to, 1807. I am indebted to my friend Mr. Tulk, the able translator of 'Wagner's Comparative Anatomy,' for the opportunity of perusing this most suggestive and original essay, which does not exist in either the Library of the British Museum, that of the College of Surgeons, or that of the Medico-Chirurgical Society. Mr. Tulk is at present engaged in the arduous task of translating the "Lehrbuch der Natur-philosophie" of Oken for the 'Ray Society.'

"Now," says Oken, "take the ear-vertebra from a fœtus of any mammal or of man, place near it an immature dorsal vertebra, or the third cervical of a crocodile, and compare the pieces of which they consist, their form, their contents, and the outlets for the nerves.

"According to Albinus and all anthropotomists, each vertebra of the fœtus consists of three distinct parts—the body and the two neurapophyses (bogentheile). You have the same in the occipital bone, but more clearly and more distinctly: the 'pars basilaris' is separated as the body of the vertebra from the 'partes condyloideæ,' which form the lateral parts: these are still more distinct from the 'pars occipitalis' which forms the spinous process: even this part is often bifid, like the spinous processes in *spina bifida*."

"Since then the foramen magnum is the hinder or lower opening of a vertebral canal, the condyles true oblique vertebral processes, the foramen lacerum an intervertebral foramen, and the crista occipitalis a spinous process, proved to be such by both its position and the muscles inserted into it,—since lastly the whole occipital bone in relation to its form as well as its function—inclosing the cerebellum as a production of the spinal chord,—is a true and in every sense characteristic vertebra, it is unnecessary to dwell more diffusely on parts, the bare mention of which suffices to make their nature recognizable."—*ib.* p. 7.

This will serve as an example of the close observation of facts, the philosophical appreciation of their relations and analogies, and, in a word, of the spirit in which Oken determines the vertebral relations of the cranial bones of the skull: and I refer to TABLE II. for his conclusions as to the parts of the second and third cranial vertebræ.

Reverting to the petrosal, Oken thus beautifully and clearly enunciates its essential nature and homology:—"You will say I have forgotten the 'pars petrosa.' No! It seems not to belong to a vertebra, as such; but to be a 'sense-organ' (Sinnorgan), in which the vertebral- or ear-nerve loses itself; and, therefore, is as distinct an organ from a vertebral element as is any other viscus (Eingeweide), or as is the eyeball itself. The (cause of) delusion (as to the homology of the petrosal) lies in this, viz. that it must be ossified agreeably with its nature (wesen), just as the eye must be crystallized."

Although Oken does not in this essay formally admit a fourth vertebra anterior to the 'eye-vertebra,' he recognises the vertebral structure as being carried out rudimentally or evanescently, by the vomer, as the prolongation of the cranio-vertebral bodies, by the lacrymal bones, as their neurapophyses, and by the nasal bones, as the spinous process. His ideas of a vertebra have evidently at this period not extended beyond the ordinary anthropotomical one of centrum and neural arch with its transverse, oblique, and spinous processes. When he indicates (beautifully and truly) the general homology of the palatine bones, as pleurapophyses, under the name of anchylosed or immoveable ribs of the head, it has reference to the transcendental idea of the repetition in the head of all the parts of the body. Thus the squamosal in mammals and the tympanic in birds represent the 'scapula' of the head, and at the same time, also, the ilium. The homologue of the squamosal (fig. 21, 27) in the bird is the 'humerus capitis': the malar (26) and the maxillary (21) are the 'oberarm' (radius and ulna capitis): the premaxillary (22) is the 'manus capitis.' The segments of the hind limb are represented by divisions of the compound lower jaw in the crocodile and embryo bird (see Table, No. III.). The pterygoids (24), the essential distinction of which from the sphenoid Oken clearly recognises, are his 'claviculæ capitis.' Oken hints at, without accepting, the (serial) homology of the hyoid arch with the pelvis; but he regards the stylohyal (38) as the 'sacrum capitis' (*ib.* p. 16).

The year after the publication of Oken's famous 'Introductory Lecture,' Prof. Duméril, apparently unacquainted with its existence, communicated to the French Institute a memoir entitled 'Considérations générales sur l'analogie qui existe entre tous les os et les muscles du tronc dans les animaux,' the second paragraph of which is headed "De la tête considérée comme une vertèbre, de ses muscles et de ses mouvements." In this paragraph, repeating the homological correspondences, demonstrated by Oken, between the basioccipital as a vertebral centrum, the condyles as 'oblique processes,' and the occipital protuberance as a spinous process, he adds, that the mastoid processes are entirely conformable to transverse processes. And M. Duméril has, I believe, here the merit of having first enunciated the general homology of the mastoids, although he does not aim at showing to which vertebral segment of the skull they properly belong. Nor, indeed, with the exception of an observation that "very often the body of the sphenoid, like the 'apophyse basilaire' of the occiput, resembles the body of a vertebra," does he push the transcendental comparisons further. Geoffroy St. Hilaire tells us*, that even the moderate and very obvious illustrations of the general homologies of the cranial bones, which M. Duméril deduced from the anatomy of the occiput, excited an unfavourable sensation in the bosom of the 'Académie;' and that the phrase 'vertèbre pensante,' which a facetious member proposed as an equivalent for the word 'skull,' and which circulated, not without some risibility, along the benches of the learned during the reading of the memoir, reaching the ears of the ingenious author, the dread of ridicule checked his further progress in the path to the higher generalizations of his science, and even induced him to modify considerably many of the (doubtless happy) original expressions and statements in the printed report, so as to adapt it more to the conventional anatomical ideas of his colleagues.

As the truth of Oken's generalization began to be appreciated, it was remembered, as is usually the case, that something like it had occurred before to others. Autenrieth and Jean-Pierre Frank had alluded, in a general way, to the analogy between the skull and the vertebral column: Ulrich, reproducing, formally, Oken's more matured opinions on the cranial vertebræ, says, "Kielmeyerum præceptorem pie venerandum quamvis vertebram tanquam caput integrum considerari posse in scholis anatomicis docentem audivi." And the essential idea was doubtless present to Kielmeyer's mind, though he reversed M. Duméril's proposition, and, instead of calling the skull a vertebra, he said each vertebra might be called a skull. But these anticipations detract nothing from the merit of the first definite proposition of the theory. It would rather be an argument against its truth, if some approximative idea had not suggested itself to other observers of nature, who only lost the merit of developing it, from not appreciating its full importance. He, however, becomes the true discoverer who establishes the truth: and the sign of the proof is the general acceptance. Whoever, therefore, resumes the investigation of a neglected or repudiated doctrine, elicits its true demonstrations, and discovers and explains the nature of the errors that have led to its tacit or declared rejection, may calmly and confidently await the acknowledgments of his rights in the discovery.

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* Annales des Sciences Naturelles, t. iii. 1824, p. 177.

It has been unfortunate for Oken, that, with one exception—the gifted Bojanus—his successors in the development of the vertebral theory of the skull have hitherto exaggerated rather than retrenched the errors of their guide. Spix[*] lends an almost servile aid to Oken in endowing the artist's symbol of the cherub with all that it seems most to want, a thorax, abdomen and pelvis, arms, legs, hands and feet. He adopts Oken's original number and composition of the cranial vertebræ, and gives them new names, which being dissociated from Oken's peculiar idea of the essential subserviency of the cranial segments to certain organs of sense, are likely to be retained.

Bojanus[†] seems first to have determined the true elements of the neural arch of the nasal vertebra; and was as happy in perceiving the pleurapophysial relations of the tympanic pedicle, as Oken had been in reference to the palatine bone. He was less accurate in his idea of the vertebra to which it belonged. The analysis of Bojanus' craniovertebral system given in Table III. precludes the necessity of dwelling upon it in the brief historical sketch here attempted.

The modifications of his original idea which Oken has introduced into his edition of the 'Natur-philosophie' of 1843, bring it into close accordance with that of Bojanus, excepting that Oken conceives the cranial neurapophyses to answer also to ribs:—"An den Seiten eines jeden Körpers liegen Flügelfortsätze, welche den Querfortsätzen der Halswirbel oder den Rippen entsprechen: 'die Gelenkköpfe des Hinterhauptsbeins' (exoccipitals), 'die grossen' (ali-) 'und kleinen Flügel' (orbito-sphenoids), 'und die beiden Seiten des Siebbeins' (prefrontals)," p. 304. With regard to the facial bones of the skull, Oken still includes the explanation of their general homology in his original idea, that "the head is (a repetition of) the whole trunk with all its systems. . . . . The encephalon is the myelon (rückenmark); the cranium, the vertebral column; the mouth is intestine and abdomen; the nose, lungs and thorax; and the jaws, limbs (glieder)."—*Op. cit.* p. 300. An idea which vitiated his original essay, and which has had the effect of obscuring a great truth in nature in the smoke of a sacrifice to a false system.

This seems the place to notice a virtual testimony to the general accuracy of the Okenian cranial system, published in 1816 by the present eminent osteologist who holds the chair of Comparative Anatomy in the 'Jardin des Plantes.' In a note to his 'Prodrome d'une Nouvelle Distribution Systématique du Règne Animal,' published in the 'Bulletin des Sciences par la Société Philomathique,' 1816, p. 105, M. de Blainville says, "J'essayerai de montrer (!) que la tête dans les animaux vertébrés est composée, 1° d'une suite d'articulations ou de vertèbres soudées, chacune développée proportionnellement au système nerveux particulier qu'elle renferme, comme dans le reste de la colonne vertébrale; 2°, d'autant d'appendices paires qu'il y a de ces fausses vertèbres, et pouvant avoir des usages différens" (p. 108). M. de Blainville does not (like Bojanus) expressly mention the general homology of any of these appendages to the ribs, or parial appendages of the true vertebræ; but he leaves it to be so understood by his subsequent enumeration and classification of the 'appendices paires ou symmétriques,' which he describes as being always in relation with a vertebra or median piece. He says, *e.g.* "Ils peuvent être divisés en simples ou en composés, ou peut-être d'après leurs usages. Les appendices simples sont les côtes. Les appendices composés sont les membres, les mâchoires, les appareils des organes des sens, le styloïde, les branches de l'hyoïde, qui sont ordinairement formés d'un plus ou moins grand nombre de pièces placées bout à bout. Quelquefois ces appendices sont libres à leur extrémité, d'autres fois ils se réunissent dans la ligne médiane inférieure en entr'elles, ou au moyen d'une pièce médiane, qu'on peut comparée, jusqu'à un certain point, au corps des vertèbres; d'ou il résulte ce qu'on nomme 'sternum' dans les mammifères, appareil branchial des poissons, hyoïde, sternum des oiseaux," etc. (*ib.* 1817, p. 110). Reserving the consideration of some of these propositions for a subsequent chapter of the present work, I shall only notice, *en passant*, the complete concordance between these views of the general homology of the locomotive members with those which Oken expresses with his usual aphoristic brevity:—"Freye Bewegungsorgane können nichts anderes als frey gewordene Rippen seyn."

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[*] Cephalogenesis, fol. 1815.

[†] Isis, 1818, and 'Parergon' in the 'Anatome Testudinis Europææ,' fol. 1821.

Cuvier includes amongst the general characters of the class *Mammalia* the arrangement of their cranial bones into three annular segments, corresponding essentially with those of which Oken had demonstrated the vertebral relations. "Leur crâne se subdivise comme en trois ceintures formées; l'antérieure, par les deux frontaux et l'ethmoïde; l'intermédiaire, par les pariétaux et le sphénoïde; la postérieure, par l'occipital: entre l'occipital les pariétaux et le sphénoïde, sont intercalés les temporaux, dont une partie appartient proprement à la face[*]."

What M. de Blainville (1816) pledges his efforts to demonstrate, Oken (Isis, 1817) was exulting in the reception of, 'not only in Germany but all Europe.' "Seit Erscheinung dieser Schrift und nun 10 Jahre verflossen.—Man spricht nun von Kopfwirbeln, Kopfarmen und Füssen, von Bedeutung der einzelnen Skeletknochen wie von einer uralten Sache; die schon in der Bibel und den Propheten gestanden," p. 1204. The chief differences, as compared with Oken's definition, are, that Cuvier, finding the frontal arch to rest upon both ethmoïd and presphenoid, assigns to the former bone the completion of the anterior cranial cincture below; and completes, in like manner, the parietal cincture by the sphenoid in its anthropotomical sense, making no distinction between the anterior and the posterior divisions of the bone. Cuvier does not apply this principle of arrangement of the cranial bones to the skull of the lower classes of vertebrata (in which, nevertheless, it is more clearly manifested than in mammals): in generalising on the constitution of the vertebrate skull, he classifies the bones, after the anthropotomists, into 'those of the cranium which encompass the brain, and those of the face, which consist of the two jaws and the receptacles of the organs of sense.'[†] With regard to the skull of fishes, in which Bojanus had found so clear an illustration and confirmation of the Okenian views, Cuvier merely says, it is almost always divisible into the same number of bones as that of other ovipara. The frontal is composed of six pieces; the parietal of three; the occipital of five; five of the pieces of the sphenoid and two of each of the temporals remain in the composition of the cranium[‡].

In his great works the 'Histoire des Poissons' and the 'Leçons d'Anatomie Comparée,' posthumous edition, Cuvier expresses more decidedly his objections to the views of the segmental or vertebral structure of the skull.

Göthe, in a small fasciculus of 'Essays of Comparative Anatomy,' which he published in the year 1820, entitles the 8th, "Can the bones of the skull be deduced from those of the vertebral column, and thence receive an explanation of their forms and functions?" He states that the idea of the three facial vertebræ occurred to him in the year 1790, prior to which time he says "die drei hintersten erkennt ich bald." The idea is developed in his essay as follows:—"The skull of mammalia is composed of six vertebræ; three for the hinder division inclosing the cerebral treasure; three composing the fore part which opens in presence of the exterior world, which it seizes and introduces.

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[*] Règne Animal, 8vo, 1817, t. i. p. 62.

[†] "La tête est formée du crâne, qui renferme le cerveau, et de la face, qui se compose des deux mâchoires et des receptacles des organes des sens."—Règne Animal, i. ed. 1817, p. 62; ed. 1829, p. 52.

[‡] *l. c.* ii. (1817), p. 107; (1829), p. 128.

"The first three vertebræ are admitted (he alludes to Oken and Spix): they are,—

"The occipital.

"The posterior sphenoid.

"The anterior sphenoid.

"The three others are not yet admitted; they are,—

"The palatine bone.

"The upper maxillary.

"The intermaxillary.

"If some of the eminent men who ardently cultivate this subject should feel interested by this simple enunciation of the problem, and would illustrate it by some figures indicating by signs and ciphers the mutual relations and secret affinities of the bones, its publication would strongly draw the thinking mind in that direction, and we may, perhaps, one day, ourselves give some notes on the mode of considering and treating these questions."

Professor Carus of Dresden has best responded to this appeal of his immortal countryman: but it must be admitted that the detailed and complex exposition of the theory of the six vertebræ and intervertebræ, of which the general results are given in Table III., have yielded to anatomical science a result which is hardly equivalent to the zeal and pains manifested in the attempt, or to the artistic merit of the illustrations, published by the accomplished author of the 'Urtheilen des Knochen und Schalengerüstes' (fol. 1828).

Geoffroy St. Hilaire deems the skeleton of the head to be composed of seven vertebræ; and he has the merit of having more steadily sought the homologies of the inferior arches of the cranial vertebræ than his predecessors, who seem not to have sufficiently appreciated the essential character of these portions of the primary segments of the vertebrate endo-skeleton. Nevertheless it must be admitted that Cuvier has made good the grounds of his rejection of Geoffroy's theory, as one based less on observation than on purely *à priori* views, according to which the bones of the skull, real or imaginary, are arranged into seven vertebræ, composed of nine pieces each*. The cranio-vertebral system of Geoffroy is liable to the further objection, that he has combined, as in the case of his typical vertebra from the tail of the flounder, parts of the exo-skeleton (*e.g.* the suborbitals) with parts of the endo-skeleton to which alone the vertebral theory is applicable.

In the fasciculi of the magnificent 'Ostéographie' with which Professor de Blainville has enriched his science, the descriptions follow the plan of the classification of the bones of the skeleton propounded in the above-cited Memoirs in the 'Bulletin des Sciences' for 1816 and 1817. In the Prospectus of the 'Ostéographie', M. de Blainville briefly refers to the great questions of comparative anatomy, which the German organologists have comprehended under the name of '*Signification of the Skeleton*,' in allusion only to the "gross errors and opinions almost extravagant, of some of the persons who have occupied themselves with these questions:" whilst he reprobates, on the other hand, in equally general terms, "those who have been unable to elevate themselves to these kind of questions, partly on account of the nature of their minds, partly from the want of proper and sufficient subjects of contemplation *."

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* Cuvier, Histoire des Poissons, 4to, t. i. p. 230.

Neither the first step, the most difficult of all, nor any of the succeeding steps in the acquisition of such views of the 'Signification of the Skeleton' as M. de Blainville adopts are noticed: no objection to the vertebral system of the skull is answered: no error that may have opposed itself to a reception of the doctrine is explained or refuted: of the particular labours and discoveries of individual homologists the author of the 'Ostéographie' is silent. He defines a vertebra, in the language of anthropotomy, as a single bone:—"Une vertèbre, considérée d'une manière générale, et par conséquent dans son état complet, est un os court, médian, symmétrique, formant un corps, partie principale de la vertèbre, aux deux faces opposées de laquelle, externe ou dorsale, interne ou ventrale, s'applique un arc plus ou moins développé, d'ou résultent deux canaux, l'un au dos, l'autre au ventre." (*ib.* *fasc.* i. p. 6.) We discern the influence of the ideas of his ingenious contemporary, Geoffroy St. Hilaire, in the admission of the ventral or inferior, as well as the dorsal or superior arch; and, like Geoffroy, he recognises the physiological relation of the upper arch to the protection of the nervous system, and that of the lower arch to the protection of the vascular system: but, overlooking or rejecting the idea of the relation of the ribs as the inferior protecting arches of the expanded central organ of the vascular system, he considers the ventral (hæmal) arches as arriving at their maximum of development in the tail. The dorsal and thoracic vertebræ are, accordingly, characterized as those which are provided with costiform appendages diversely articulated to them; overlooking, I may remark, the costal appendages of the cervical vertebræ in the saurians and those which become anchylosed to the cervical vertebræ in birds, as do, frequently, their serial homologues to the dorsal vertebræ in the same class. M. de Blainville seems, also, wholly ignorant of the fact that the bent-forward ends of the long transverse processes of the lumbar vertebræ of the hares, cavies, and many other rodents, are primarily developed as distinct costal rudiments: the same rudiments of lumbar ribs are found in the fœtus of the hog, and in the first lumbar vertebra of many mammals †. "Les lombaires," says M. de Blainville, "n'ont plus de côtes, même incomplètes."

The ribs not being regarded as essentially parts of the inferior or hæmal arches of vertebræ, the sternal bones which complete these greatly expanded arches are accordingly regarded as a distinct series of bones, and called 'sternebers.' M. de Blainville, as we have seen, had before (1817) compared them to vertebral bodies. In the 'Ostéographie,' however, he rightly regards the body of the hyoid as their serial homologue, but does not extend his comparison to the bones that in like manner complete the mandibular and maxillary arches. These, with the cornua of the hyoid, and the sternal and vertebral ribs, he classes with the bones of the extremities, under the name of appendages (appendices), adopting, in his larger work, as in his original essay, essentially the idea of Oken, that the locomotive members are liberated ribs.

The Typical Vertebra.—After much additional research and comparison since the first publication of my ideas of the constitution of the typical vertebra or primary segment of the endoskeleton ‡, I have found no reason for modifying them, but have derived additional evidence of their accuracy; and I therefore reproduce the diagrammatic figure with which they were originally

* Ostéographie, Prospectus, April, 1839, p. 5.

† Thirle, in Müller's Archiv fur Physiologie, 1839, p. 106.

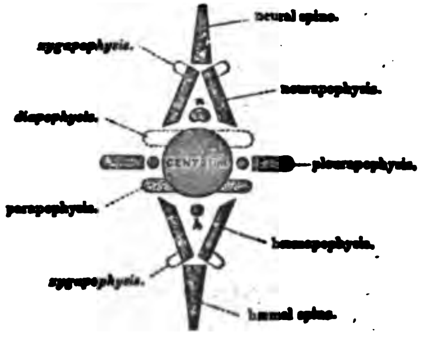
‡ Geological Transactions, 4to, 1838, p. 518.

illustrated (fig. 14). Although my investigations of the fundamental type of the vertebrate skeleton were first made upon the class of fishes, where vegetative uniformity or irrelative repetition most prevails, and where, therefore, the type is least obscured by the modification of one part in mutual subserviency with another, I soon found that I should be led astray by confining my observations to fishes, and by borrowing illustrations from that class exclusively. Comparison of the piscine skeleton with those of the higher animals demonstrates that the natural arrangement of the parts of the endoskeleton is in a series of segments succeeding each other in the axis of the body. These segments are not, indeed, composed of the same number of bones in any class or throughout any individual animal. But certain parts of each segment do maintain such constancy in their existence, relation, position, and offices, as to enforce the conviction that they are homologous parts, both in the constituent series of the same individual skeleton, and throughout the series of vertebrate animals. For each of these primary segments of the skeleton I retain the term 'vertebra'; but with as little reference to its primary signification, as a part specially adapted for rotatory motion, as when the comparative anatomist speaks of a sacral vertebra. The word may, however, seem to the anthropotomist to be used in a different or more extended sense than that in which it is usually understood; yet he is himself, unconsciously perhaps, in the habit of including in certain vertebræ of the human body, elements which he excludes from the idea in other natural segments of the same kind, influenced by differences of proportion and coalescence, which are the most variable characters of a bone. Thus the rib of a cervical vertebra is the 'processus transversus perforatus,' or the 'radix anticus processus transversi vertebræ colli'*: whilst in the chest, it is 'costa,' or 'pars ossea costæ.' But the ulna is still an ulna in the horse, although it be small and anchylosed to the radius.

The osteology of man, therefore, cannot be fully or rightly understood until the type of which it is a modification is known, and the first step to this knowledge is the determination of the vertebral segments, or natural groups of bones, of which the myelencephalous skeleton consists.

I define a vertebra, as *one of those segments of the endo-skeleton which constitute the axis of the body, and the protecting canals of the nervous and vascular trunks*: such a segment may also support *diverging appendages*. Exclusive of these, it consists, in its typical completeness, of the following elements and parts:—

Fig. 14.



Ideal typical vertebra.

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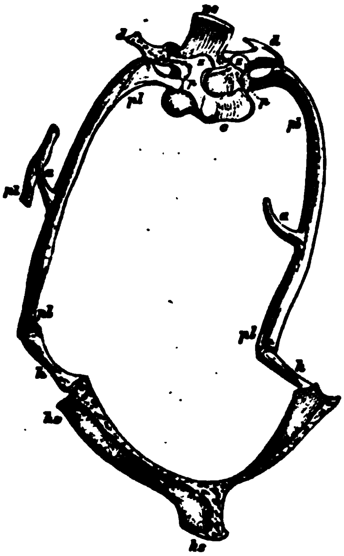
* Soemmerring, De Corporis Humani Fabricâ, 1794, i. p. 239.

The names printed in roman type signify those parts which, being usually developed from distinct and independent centres, I have termed 'autogenous' elements. The italics denote the parts, more properly called processes, which shoot out as continuations from some of the preceding elements, and are termed 'exogenous': *e.g.* the diapophyses or upper 'transverse processes,' and the zygapophyses, or the 'oblique' or 'articular processes' of human anatomy.

The autogenous processes generally circumscribe holes about the centrum, which, in the chain of vertebræ, form canals. The most constant and extensive canal is that (fig. 14, *n*) formed above the centrum, for the lodgment of the trunk of the nervous system (neural axis) by the parts thence termed 'neurapophyses.' The second canal (fig. 14, *h*), below the centrum, is in its entire extent more irregular and interrupted; it lodges the central organ and large trunks of the vascular system (hæmal axis), and is usually formed by the laminæ, thence termed 'hæmapophyses.' At the sides of the centrum, most commonly in the cervical region, a canal is circumscribed by the pleurapophysis or costal process, by the parapophysis, or lower transverse process, and by the diapophysis, or upper transverse process, which canal includes a vessel, and often also a nerve.

Thus a typical or perfect vertebra, with all its elements, presents four canals or perforations about a common centre; such a vertebra we find in the thorax of man and most of the higher classes of vertebrates, also in the neck of many birds. In the tails of most reptiles and mammals, the hæmapophyses (as in fig. 14) are articulated or anchylosed to the under part of the centrum; space being needed there only for the caudal artery and vein. But where the central organ of circulation is to be lodged, an expansion of the hæmal arch takes place, analogous to that which the neural arches of the cranial vertebræ present for the lodgment of the brain. Accordingly in the thorax, the pleurapophyses (fig. 15, *pl*) are much elongated, and the hæmapophyses (fig. 15, *h*) are removed from the centrum, and are articulated to the distal ends of the pleurapophyses; the bony hoop being completed by the intercalation of the hæmal spine (fig. 15, *hs*) between the ends of the hæmapophyses. And this spine is here sometimes as widely expanded (in the thorax of birds and chelonians, for example) as is the neural spine (parietal bone or bones) of the middle cranial vertebra in mammals. In both cases, also, it may be developed from two lateral halves, and a bony intermuscular crest may be extended from the mid-line, as in the skull of the hyæna, and the breast-bone of the bird (fig. 15, *hs*). To facilitate the comparison of the merits of the preceding view and nomenclature of the typical vertebra with those of other comparative anatomists, I have thrown the results into the form given in Table II.

Fig. 15.



Natural typical vertebra: thorax of a bird.

To the question why I should have invented new names when Geoffroy St. Hilaire had already proposed others for the vertebral elements, I can only repeat the regret with which I found myself compelled to that invidious step, after having arrived at the conviction, that the learned Parisian Professor had sometimes applied the same term to two distinct elements, and sometimes two distinct names to one and the same element: and I am glad to be able to cite the authority of Cuvier for the propriety and advantage of such a step. His words are in reference to an analogous case, "Donner à un mot connu un sens nouveau est toujours un procédé dangereux, et, si l'on avoit besoin d'exprimer une idée nouvelle, il vaudroit encore mieux inventer un nouveau terme, que d'en détourner ainsi un ancien[*]." Now there is scarcely one term in the first column in Table II. which is synonymous with its opposite in the second column, or which expresses exactly the same idea; and the discrepancy becomes greater in regard to the terms applied to the vertebral elements of the head, in columns 1 and 5 of Table III. The respective concordance of the views of the vertebral archetype entertained by Geoffroy and myself with Nature will be determined and judged of by succeeding impartial and original observers.

With regard to the term *cycléal*, "de κύκλος, cercle, pour rappeler sa forme annulaire, permanentes chez les premiers," (Articulata, Dermovertébrés, Geoff.) "et, au contraire, non persévérante chez les derniers" (Vertebrata, Hauts-vertébrés, Geoff.), it is understood by its author to apply to the annular segment of the crust of the insect, as well as to the 'centrum' of the endoskeletal vertebra. Geoffroy's primary division of the parts of a vertebra is into the centre or nucleus (noyau) and the lateral branches. The upper 'branches laterales' or 'périaux' are equivalent to my neurapophyses and also to my neural spine, in fishes: the lower lateral branches or 'paraaux' are sometimes free and floating[†], when they answer to my 'pleurapophyses'; but they are sometimes so united as to form a canal, when they answer to my 'parapophyses' in the tail of fishes[‡], and to my 'hæmapophyses' in the tail of cetaceans. Geoffroy supposed, for example, that the hæmal canal in the tail in all fishes was formed by the ribs, bent down and anchylosed at both ends[§], and that the hæmal canal in the tail of the crocodile and whale was constituted by a like metamorphosis of the same vertebral elements. He, also, argued that, as the small spinal chord of fishes did not demand so great a development in breadth of the neurapophyses, they were permitted to attain to unusual length; and that, coalescing together, they thus constituted not only the neural arch but the neural spine, to which latter, therefore, he extended the name 'périal'; whilst to the corresponding part in mammals he gives the name of 'épial'. But, again, in fishes, he calls the dermal spines developed in the embryonic median fold of integument which is metamorphosed into the dorsal fins, 'épiaux'; and the corresponding dermal spines of the ventral fin 'cataaux.' The lepidosiren, however, manifests the neural spine distinct from both the neurapophyses below and the dermo-neural spine above: and such neural spine is unequivocally homologous with the anchylosed neural spine in osseous fishes[‖]. It is quite in harmony with the position of the class of fishes at the bottom of the vertebrate scale that they should present a greater degree of calcification of the parts belonging to the same category of the skeletal system as the shells and crusts of the invertebrates: hence it is that whilst the median dermal fins of the marine mammalia have

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[*] Mémoires du Muséum, t. xx. p. 123.

[†] As they are illustrated in the abdominal vertebra of the fish figured by Geoffroy in the 'Mémoires du Muséum,' t. ix. (1822), pl. 5, fig. 4, polypterus, e.

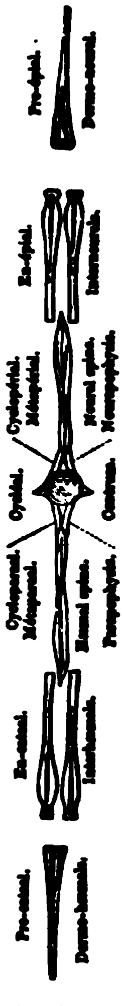
[‡] *Ib.* fig. 2, e a.

[§] This occurs as an exceptional condition, in the lepidosteus, and perhaps in the lepidosiren.

[‖] Linn. Trans. vol. xviii. p. 23, fig. 4, e, d.

their supporting skeleton in the primitive histological fibrous state, the corresponding parts are ossified in fishes: rarely, however, are such parts in answerable number to the vertebræ; and the true spines of these vertebræ, when the median fins and their bony spines are removed, in fishes, show as little indication of the place or existence of such fins, as do the vertebræ in the porpoise of the existence of its dermal fin. In proportion as ossification has extended into the dermal system of fishes it has been arrested in the vertebræ, which in the trunk and tail of fishes present their least complex condition. Two of the autogenous elements, the 'hæmapophyses,' are absent, and are commonly represented, in the tail, by the modified 'parapophyses.' The seeming complexity of a fish's vertebra arises from the intercalation of bones appertaining to the system of the dermo-skeleton: it would have been an unusual exception to the general course of development if the lowest of the vertebrate classes should have presented the vertebral skeleton in its highest state of complication; and Geoffroy St. Hilaire was unfortunate in taking a fish's vertebra with its extrinsic evertebrate complications, as the perfect type of that primary segment of the myelencephalous skeleton (fig. 16). He was still more unlucky in having for the subject of his figure* a specimen from which two of the pieces had been accidentally lost, as Cuvier afterwards pointed out; yet Geoffroy's mutilated caudal vertebra of the plaice continues to be copied in some compilations of comparative anatomy, as the type of a vertebra! To obtain the dermal spines (pro-epial and pro-cataal) of the vertically extended caudal vertebræ of fishes, Geoffroy had recourse to a hypothetical division lengthwise of the interneural and interhæmal spines (which are represented as being single in his figure), and to as gratuitous a displacement of one of the halves from the side to the summit of the other †. Now the interneural and interhæmal spines are actually double in relation to the neural and hæmal spines; yet they coexist with a dermoneural and dermohæmal ray, which therefore needs no imaginary change of place of either of its supporting spines to account for its existence. I subjoin in fig. 16 an entire vertebra answering to the mutilated one figured by Geoffroy; and for the better understanding of the difference between his determinations of the vertebral elements and those given in the present work, the names respectively indicating those different determinations are added to the figure. In the description of the plate in the 'Mémoires du Muséum,' Geoffroy explains that the 'pro-épial' is the left half or 'épial *gauche*,' and the en-épial the right half or 'épial *droit*': that the en-cataal is the right half or 'cataal *droit*,' and the pro-cataal the left half or 'cataal *gauche*,' of his imaginarily divided epivertebral and catavertebral elements (*l. c.* p. 115).

Fig. 16.



Endo- and exo-skeletal elements of a caudal vertebra of a Plaice (*Pleuronectes*).

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* Mémoires du Muséum, t. ix. (1822), pl. 5, fig. 1.

† "L'une de ces pièces monte sur l'autre"—"l'une se maintient en dedans, quand l'autre s'élance en dehors," *ib.* p. 97.

The trunk of fishes, in respect of its viscera and the degree of development of the endoskeleton, answers to the lumbar and caudal regions of air-breathing vertebrates, where the vertebræ usually lose some of their elements, at least as bones. The heart and respiratory organs are placed in the head of the fish; and it is only in this region that the vertebral segments attain to typical completeness in that class. Geoffroy, in studying the special and general homologies of the bones of the head of fishes, blends indiscriminately, as in the supposed typical vertebra from the tail, elements of the dermoskeleton (suborbitals and lacrymals, *e. g.*) with those of the endoskeleton; and also presses the capsules of the special organs of sense into the composition of the seven cranial vertebræ of his system. It needs only to compare the synonyms of the elements of these vertebræ in Table III. to perceive how impossible it would have been to have expressed the ideas which I wish to expound and illustrate in the present work by the use of the names for the vertebral elements proposed by Geoffroy, or of english equivalents. The prefrontals, *e. g.* (no. 14), which I regard as the neurapophyses of the nasal vertebra, are, according to Geoffroy, epials of the 2nd or labial vertebra in the class of fishes; but are epials of the 1st or nasal vertebra in the crocodile, according to the tables given in the 'Annales des Sciences,' t. iii. pl. 9, and 'Atlas,' p. 44; whilst they are the perials of the 2nd vertebra in the scheme of 1825, cited in the fifth column of Table III.

I have deemed it requisite to enter the more fully into the grounds for abandoning the analysis and nomenclature of the typical vertebra proposed by Geoffroy, because they have received the sanction in this country of the learned Professor of Comparative Anatomy at University College. Dr. Grant[*] converts the French names into English equivalent phrases; 'cyclo-vertebral element' for *cycléal*, 'perivertebral element' for *périal*, &c.; and abandons the advantage of a definite name, without remedying the disadvantages of the double employment of the same names for two distinct elements, and of the application of different phrases for the same element. If, for example, the neural spine of the reptile or mammal be, in nature, the homologue of the neural spine of the fish, then the latter is called an 'epivertebral element,' whilst the former is called a 'perivertebral element.' If the dermo-neural spines of the dorsal fin of a fish be, in nature, homologous with the fibro-ligamentous tissue supporting the dorsal fin of the dolphin, then the term 'epivertebral element' is applied to a spine of the exoskeleton in the fish, and to a spine of the endoskeleton in the mammal, which spine co-exists with such dermal spine in the fish (see fig. 16). If the parapophysis or inferior transverse process in the fish be a distinct element from the diapophysis or superior transverse process in the mammal, the same phrase, 'paravertebral element,' is applied to each. Dr. Grant, moreover, gives the same name, 'catavertebral elements,' to the free vertebral ribs in fig. 28, B. *g.* p. 58, *op. cit.*, as he applies to the hæmapophyses in the tail of the reptile or cetacean, in fig. 28, C. *g.* *loc. cit.*; whilst Geoffroy applies the name 'cataaux' to the sternal ribs, and not to the vertebral ribs: as the caudal vertebræ of the menopome (fig. 28), show that it is with the sternal ribs that the chevron bones in the tails of reptiles and cetaceans are homologous, both parts are 'hæmapophyses' in my system. The transference of the term 'catavertebral elements' (for *cataaux*), from the 'côtes sternales' to the pair of ribs extended from the ends of the parapophyses of the abdomen of fishes, is a deviation from the original vertebral system of Geoffroy, which seems to lead further away from nature. If it is meant that the outstretched parapophyses in the diagram of the abdominal vertebra of a fish (fig. 28, B. *f. f.* *loc. cit.*), and which are there called 'paravertebral elements,' are the homologues of the 'côtes vertébrales' of higher vertebrates, to which Geoffroy assigned the name 'paraaux,' this appears to be another misapprehension of the relations in question.

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[*] Outlines of Comparative Anatomy, 1835, pp. 57–58.

Development of vertebræ.—Before applying the idea of the archetypal vertebra, or primary segment of the endo-skeleton, given in figs. 14 and 15, to the elucidation of the modifications of those segments in the different vertebrate classes, I shall premise a few observations on the mode of development of the vertebræ in those classes.

The chief condition of the development of distinct vertebræ in the trunk is the conjunction of nerves with, or their progress from the spinal chord: at least, this circumstance, with the concomitant exit of blood-vessels from the neural canal, seems to determine the development of the neurapophyses: and the vertebral bodies are not slow in coinciding in number with those important arches; and in determining with the regular primary pairs of (intercostal, lumbar, &c.) arteries, the inferior or hæmal arches. We may learn how much the development of the neurapophyses and vertebral bodies depends, in the trunk, upon the conjunction of nerves with the spinal chord, by the fact that, in the regenerated tails of lizards, the vertebral axis remains continuous and unjointed, because there is no co-extensive spinal chord giving off pairs of nerves.

An extremely delicate fibrous band, with successively accumulated gelatinous cells, compacted in the form of a cylindrical column, and inclosed by a membranous sheath, is the primitive basis, called 'notochord'* (*chorda dorsalis* seu *gelatinosa*, Lat., *gallertsäule* und *ruckensaite*, Germ.), in and around which are developed the cartilaginous or osseous elements by which the vertebral column is established in every class of *Myelencephala*.

The earlier stages of vertebral development are permanently represented, with individual peculiarities superinduced, in the lower forms of the class of fishes†. In the *Dermopteri* or cyclostomous fishes, the neural and hæmal canals are formed by a separation of the layers of the outer part of the aponeurotic sheath of the gelatinous chorda: in the lancelet (*Amphioxus*) there is no distinction of structure in the cranial part supporting the anterior end of the neural axis, with which the trigeminal, optic and olfactory nerves communicate, and the rest of the rudimental vertebral column: a labial cartilaginous arch supporting the tentacula is, at least, the only lineament of development which sketches out the skull. In the myxinoids the skull includes a complex system of cartilages, but the vertebral column of the trunk has not advanced beyond the gelatino-aponeurotic stage. In the lamprey cartilaginous laminæ are developed in the outer layer of the fibrous sheath, and give the first indication of neural arches‡. In the sturgeons (*Sturio*, *Polyodon*) the inner layer of the fibrous capsule of the gelatinous notochord has increased in thickness, and assumed the texture of tough hyaline cartilage. In the outer layer are developed distinct, firm, and opake cartilages, the neurapophyses, which consist of two superimposed pieces on each side, the basal portion bounding the neural canal, the apical portion the parallel canal filled by fibrous elastic ligament and adipose tissue; above this is the single cartilaginous neural spine. The parapophyses are now distinctly developed, and joined together by a continuous expanded base, forming an inverted arch beneath the notochord for the vascular trunks, even in the abdomen. Pleurapophyses are articulated by ligament to the ends of the laterally projecting parapophyses in the first twelve or twenty abdominal vertebræ: in the anterior ones these 'vertebral ribs' are composed of two or three distinct cartilages*: the posterior pleurapophyses are short and simple. The parapophyses gradually bend down to form hæmal arches in the tail, at the end of which we find hæmal cartilaginous spines corresponding to the neural spines above. The tapering anterior end of the notochord is continued forwards into the basal elements of the cranial vertebræ. Vegetative repetition of perivertebral parts not only manifests itself in the composite neurapophyses and pleurapophyses, but in a small accessory (interneural) cartilage, at the fore and back part of the base of the neurapophysis; and by a similar (interhæmal) one at the fore and back part of most of the parapophyses†.

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* Νῶτος *back*, χορδὴ, *string*. We have hitherto had no English equivalent for this embryonic keel or basis of every vertebrate animal: 'dorsal chord' or 'chorda' is liable to be misunderstood for the 'spinal chord.'

† Hunterian Lectures on Vertebrata, 1846, pp. 45, 46.

‡ Cuvier, Mémoires du Muséum d'Histoire Naturelle, t. i. 1815, p. 130.

Amongst the sharks (*Squalidæ*) a beautiful progression in the further development of a vertebra has been traced out, chiefly by J. Müller‡. In *Heptanchus* (*Squalus cinereus*) the vertebral centres are feebly and vegetatively marked out by numerous slender rings of hard cartilage in the notochordal capsule, the number of vertebræ being more definitively indicated by the neurapophyses and parapophyses; but these remain cartilaginous. In the piked dog-fish (*Acanthias*) and the spotted dog-fish (*Scyllium*) the vertebral centres coincide in number with the neural arches, and are defined by a thin layer of bone, which forms the conical articular cavity at each end: the whole exterior of the centrum is covered by soft cartilage, except at the concave ends; the two thin funnel-shaped plates of osseous matter coalesce at their perforated apices, and form a basis of the vertebral body like an hour-glass; the series of these centrums protecting a continuous moniliform remnant of the gelatinous notochord. In the great basking-shark (*Selache*) the vertebral bodies are chiefly established by the terminal bony cones, the thick margins of which give attachment to the elastic capsules containing the gelatinous fluid, which now tensely fills the intervertebral biconical spaces. Four sub-compressed conical cavities extend, two from the bases of the neurapophyses, and two from those of the parapophyses, towards the centre of the vertebral body, contracting as they penetrate it. These cavities always remain filled by a clear cartilage: the central two-thirds of the rest of the vertebral body contain concentric, progressively decreasing, and minutely perforated rings or cylinders of bone, interrupted by the four depressions: the peripheral third of the vertebral body contains longitudinal bony laminæ, which radiate, perpendicularly to the plane of the outermost cylinder, to the circumference; these outer laminæ lie, therefore, parallel with the axis of the vertebra, and the intervening fissures, like those between the concentric cylinders within, are filled by clear cartilage, which shrinks, and leaves them open in the dry vertebra§.

In *Cestracion* the intermediate part of the centrum between the terminal cones is strengthened by longitudinal radiating plates only; in *Squatina* by concentric cylinders only. In the tope (*Galeus*) all the space between the terminal bony cones is ossified, except the four conical cavities, the bases of which are closed by the neur- and par-apophyses; so that the whole exterior of the centrum appears formed by smooth compact bone.

In the osseous fishes I find that the centrum is usually ossified from six points, four of which commence, as Rathke‖ describes, in the bases of the two neurapophyses and the two parapophyses; but the terminal concave plates of the centrum are separately ossified. They coalesce with the intermediate part of the centrum, which is sometimes completely ossified, but commonly a communicating aperture is left between the two terminal cones; and in many cases, the plates by which calcification attains the periphery of the body leave interspaces permanently occupied by cartilage, forming cavities in the dried vertebra, especially at their under part, or giving a reticulate surface to the sides of the centrum. The expanded bases of the neur- and par-apophyses usually soon become confluent with the bony centrum; sometimes first expanding so as wholly to inclose it, as, for example, in the tunny, where the line of demarcation may always be seen at the border of the articular concavity, though it is quite obliterated at the centre, as a section through that part demonstrates.

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* Brandt & Ratzeburg, Medizinische Zoologie, 4to, 1833, t. ii. pl. iv. fig. 1.

† Hunterian Lectures on Vertebrata, 1846, p. 53, fig. 12.

‡ See Agassiz, Recherches sur les Poiss. Foss. t. iii. pp. 361, 369.

§ Hunterian Lectures on Vertebrata, 1836, p. 55, fig. 13.

‖ Abhandlungen zur Bildungs und Entwickelungsgeschichte, Zweiter Theil, 1833, p. 41.

Müller correctly distinguishes a 'central' from a 'peripheral' (cortical) part or seat of the ossification of the vertebral bodies of fishes. The peripheral ossification which takes its rise from the outer layer of the fibrous sheath of the notochord sometimes extends into broad plates beneath the anterior vertebræ of the trunk, and tends to fix or anchylose a certain number of them; when they are commonly represented by the partially distinct central parts of the bodies, together with the neur- and par- and pleur-apophyses.

The batrachia follow closely the stages above-cited in fishes; the centrums being arrested at the biconical stage in the perennibranchiates, but converted into ball-and-socket vertebræ by the ossification of the interposed gelatinous ball[*] and its adhesion, either to the fore-part of the centrum (*Pipa*, *Salamandra*), or the back part (*Rana*, *Bufo*). The mode of ossification of the centrum varies somewhat in batrachia. Müller[†] describes annular ossifications in the sheath of the notochord of the *Rana temporaria* and *R. esculenta*, which support, at first, the neurapophyses. Dugés, apparently influenced by M. Serres' so-called 'law of centripetal development,' describes two cartilaginous nuclei, side by side; but the more obvious and better-determined development of the vertebræ of fishes gives no countenance to this bilateral beginning of ossification of the centrum as a general law. The first distinct bony nucleus in the centrum observed by Dugés was bilobed, and afterwards cubical; but excavated before and behind, as well as beneath[‡]. The ossification of the centrum is completed by an extension of bone from the bases of the neurapophyses, which effect, also, the coalescence of these with the centrum. In *Pelobates fuscus*, and *Pelobates cultripes*, Müller found the entire centrum ossified from this source, without any independent points of ossification.

The vertebræ of the tail of the larvæ of the anourans are represented distinctly only in the aponeurotic stage. Even when the change to cartilage takes place, the tendency to coalescence has begun to operate, and only two long neurapophyses are established on each side: the ossification of these plates extends into the fibrous sheath of the remnant of the coccygeal notochord, and they coalesce when the perishable parts of the tadpole-tail have been absorbed, and the fore- and hind-legs developed, constituting the long, often hollow, and inferiorly grooved coccygeal bony style.

In saurians, birds and mammals, the notochord is inclosed by cartilage before ossification begins; which cartilage is continuous with the cartilaginous neurapophyses[§]. In birds, the two histological processes, chondrification and ossification, do not precisely follow the same route. In the centrums of the dorsal and cervical vertebræ of the chick chondrification is centripetal: it begins from two points at the sides and proceeds inwards, the middle line of the under surface of the primitive notochord resisting the change longest. But, when the lateral cartilages have here coalesced, ossification begins at the middle line and diverges laterally; the primitive nuclei of the bony centres appearing as bilobed ossicles, and its direction is centrifugal. The lobes ascend to embrace the shrivelled remnant of the chorda, like the hollow vertebral centres in fishes. Only in the sacral vertebræ has ossification been seen to begin from two distinct points at the middle line. The bases of the separately ossifying neurapophyses extend over much of the centrum, and soon coalesce with it. In reptiles a greater proportion of the centrum is ossified from an independent point, and the bases of the neurapophyses often remain permanently distinct and united to the centrum by suture. In mammals, as in fishes, the centrum is ossified from an anterior and posterior centre, establishing the articular surfaces, as well as from an intermediate point. This is considerably overlapped by the bases of the neurapophyses, before they coalesce with the centrum. The three primitive parts of the centrum remain longest distinct in the cetacea. The body of the human atlas is sometimes ossified from two, rarely from three, distinct centres placed side by side *. From these ascertained diversities in the mode of formation of the central element of the vertebra, it will be seen how little developmental characters can be relied on as affecting the determination of homologous parts.

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[*] Dutrochet, Mémoires pour servir à l'Histoire Nat. et Physiol. des Animaux, &c., t. ii. p. 302. 1837.

[†] Neurologie der Myxinoiden, 1840, p. 69.

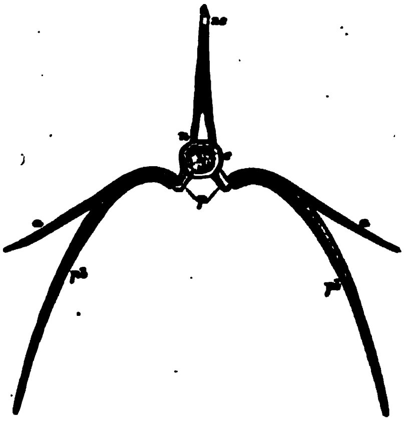
[‡] Recherches sur les Batraciens, 1835, 4to, p. 106.

[§] Müller, Vergleichende Anatomie der Myxinoiden, Neurologie, 1840, p. 74.

General Characters of Vertebræ of the Trunk.—The ossified parts of the abdominal vertebræ of osseous fishes answer to *c*, centrum; *n*, neurapophyses; *n s*, neural spine; *p*, parapophyses; *pl*, pleurapophyses; and *a*, appendages (fig. 17).

The neurapophyses commonly coalesce with their respective centrums; except in the case of the atlas, where the neural arch is sometimes quite separated from the centrum, and wedged between those of the occiput and second vertebra. I have found also the neurapophyses of the two last caudal vertebræ unanchylosed to their centrums in a large sea-perch (*Centropristis gigas*, O.) in which the five terminal hæmal arches and spines remained similarly distinct, and articulated with the centrums below. In the carp and pike, the primitive independence of both neurapophyses and parapophyses is more general and longer maintained. In the lepidosiren the vertebral bodies are not developed, the notochord being persistent; but the peripheral vertebral elements are well-ossified: the neurapophyses in this fish remain distinct from the neural spines; and the hæmal spines are in like manner moveably articulated to the hæmal arches. These

Fig. 17.



Ossified parts of abdominal vertebra, Fish.

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* Meckel, Archiv für die Physiologie, Bd. i. (1815) t. vi. fig. 1.

are formed by the gradually bent-down ribs[*], which are formed in the abdomen either by unusually elongated 'parapophyses' (if they be interpreted by the condition of those elements in the cod-fish), or by pleurapophyses articulated directly to the fibrous sheath of the notochord; which interpretation of the mode of formation of the hæmal arches is supported by Professor Müller's discovery of the nature of those arches in the *Lepidosteus*[†]. Whether we adopt the analogy of the *Anacanthini*, or the *Ganoidei* (and the general affinity of the *Protopteri* to the ganoids would incline the choice to the latter), the constitution of the hæmal arches in the lepidosiren is strictly piscine; at least if we take the skeleton of the tailed batrachia (fig. 28) as our guide to the homology of the caudal inferior arches in higher reptiles and mammals. The unusual size and length of the abdominal parapophyses in the cod-tribe (*Gadidæ*), the flat-fishes (*Pleuronectidæ*), and the genus *Ophidium*, evinces the natural character of the order *Anacanthini*, in which they have been grouped together by Professor Müller: the pleurapophyses are, conversely, very short and slender in this order. In all bony fishes the costal arch in the abdomen is completed by the aponeurotic septa between the ventral portions of the myocommata[‡], which there represent the 'hæmapophyses' (*cartilagines costæ, inscriptiones tendineæ musc. recti abdominis* of anthropotomy). Indeed, when we reflect that the trunk of the fish, by reason of the advanced position of the heart and breathing organs, answers to the abdominal and caudal regions of the trunk of higher vertebrates, we could hardly expect the typical vertebra to be there carried out in osseous tissue; but rather be prepared to find the hæmapophyses retaining the same primitive histological state which they present in the abdomen of mammals and man (fig. 25, *h''*).

Immediately behind the coracoid arch, it is usual to find a long and slender rib-like bone, sometimes composed of two pieces, on each side; it gives a firmer implantation to the portion of the myocommata immediately behind the pectoral fin; and is obviously the ossified serial homologue of the hæmapophysial aponeuroses between the succeeding myocommata. It is usually detached from its centrum and articulated superiorly to the inner side of the coracoid: when it rises higher, as in the *Batrachus*, it becomes attached to the atlas, and in the *Argyreiosus vomer* it meets and joins its fellow below, forming a true inverted or hæmal arch, parallel with, but more slender than the coracoid arch. No other idea of the general homology of this arch presents itself than as a hæmal one, completing the costal arch as an ossified hæmapophysis, differing from the typical vertebra (fig. 15) only by the nondevelopment of a sternum or hæmal spine: and there appears to be as little ground for hesitation as to the particular segment of the endoskeleton to which to refer this costal or inverted arch; its immediate succession to the corresponding arch attached to the occiput, as well as the occasional direct attachment, indicating that segment to be the atlas or first vertebra of the trunk.

The best-marked general character of the vertebral column of the trunk in the class *Pisces* is that which Professor J. Müller first pointed out; viz. the formation of the hæmal arches in the tail by the gradual bending down and coalescence of the parapophyses; the exceptions being offered by the ganoid polypterus and lepidosteus and the protopterous lepidosiren. The pleurapophyses are, sometimes, continued in ordinary osseous fishes from the parapophyses after the transmutation of these into the hæmal arches. The dory, tunny, and salmon yield this striking refutation of the idea of the formation of those arches in all fishes, by displaced, curtailed and approximated ribs. In some fishes, however (*e. g.* the cod), reduced pleurapophyses coalesce with the parapophyses to form the hæmal arches of the caudal vertebræ. The menopome, amongst the lowest or perennibranchiate reptiles, yields a clear disproof of the formation of the hæmal arch in the tail by the pleurapophyses (the parts, viz. called by Geoffroy 'paraux,' and by Dr. Grant 'catavertebral elements' in the abdomen of fishes)*. The vertebral ribs or pleurapophyses in the menopome (fig. 28, *pl*) are short and simple and suspended to the extremities of the diapophyses (*d*) at the beginning of the tail, where they coexist with hæmal arches (*h*, *h*): these must be formed, therefore, by different elements, which, since no trace of parapophyses exists in any part of the spine, I conclude to be the 'hæmapophyses.' The young crocodile and the adult enaliosaurs give the same evidence of the nature of the hæmal arches in the tail, with which the corresponding arches or chevron-bones, in cetacea and many other mammalia, are homologous.

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[*] Linn. Trans. vol. xviii. pl. 23, fig. 4, *s s*.

[†] Remarks on the Structure of the Ganoidei, in Taylor's Scientific Memoirs, vol. iv. p. 551.

[‡] Lectures on Vertebrata, 1846, p. 163, fig. 44, *h p*.

Thus the contracted hæmal arch in the caudal region of the body may be formed by different elements of the typical vertebra: *e. g.* by the parapophyses (fishes generally); by the pleurapophyses (lepidosiren); by both parapophyses and pleurapophyses (*Sudis*, *Lepidosteus*), and by hæmapophyses, shortened and directly articulated with the centrums (reptiles and mammals)†. The caudal vertebræ of some flat-fishes (*Pleuronectidæ*, fig. 16), and the murænæ, would seem to disprove the parapophysial homology of the hæmal arches in such fishes, since transverse processes from the sides of the body coexist with them, as they do in the cetacea. But, if we trace the vertebral modifications throughout the entire column in any of these fishes, we shall find that the hæmal arches are actually parts of the transverse processes, not independent elements, as in the cetacea; but due to a progressive bifurcation: this, in *Muræna Helena*, for example, begins at the end of the transverse processes of about the twenty-fifth vertebra, the forks diverging as the fissure deepens, until, at about the seventy-third, the lower fork descends at a right angle to the upper one (which remains to represent the transverse process), and, meeting its fellow, forms the hæmal arch, and supports the antero-posteriorly expanded hæmal spine. In the plaice a small process is given off from the expanded base of the descending parapophysis of the first caudal vertebra, which increases in length in the second, rises upon the side of the body in the third, becomes distinct from the parapophysis in the fourth, and gradually diminishes to the ninth or tenth caudal vertebra, when it disappears. These spurious transverse processes never support ribs.

The neurapophyses are often directly perforated by the nerves in fishes, but are sometimes notched by them, or the nerves issue at their interspaces.

The neurapophyses, which do not advance beyond the cartilaginous stage in the sturgeon, consist in that fish of two distinct pieces of cartilage; and the anterior pleurapophyses also consist of two or more cartilages, set end on end: and this interesting compound condition is repeated in cases where the pleurapophysial element is ossified and required to perform unusual functions in the bony state in other fishes. Amongst the more special or exceptional modifications of the vertebræ of the trunk of fishes, which indicate the extent to which their normal segmental character may be marked, I would cite those of the anterior vertebræ in the pipe-fishes, in the loaches, and in certain siluroids.

In the *Fistularia tabaccaria* (Pl. 1, fig. 6) the four anterior vertebræ are much elongated; the second one even to eight times the length of the ordinary abdominal vertebræ: and their centrums (*c*) are firmly interlocked together, by very deeply indented sutures. The parapophyses (*p*) are co-extended with the centrums, and overlap each other, forming a continuous outstanding horizontal ridge on each side; and the neural spines (*n s*) form a similar vertical continuous crest.

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* Outlines of Comparative Anatomy, p. 58, fig. 23, B, *g*.

† By a misconception of the sense in which I use the term 'hæmapophyses,' M. Agassiz has applied it to the laminæ of the inferior or hæmal arches in fishes. "Recherches sur les Poiss. Foss." tom. i. p. 96.

In the *Cobitis fossilis* and *C. barbatula* the par- and pleur-apophyses (*ib.* fig. 7, *p*) of the second and third vertebræ coalesce and swell out into a large 'bulla ossea' on each side, inclosing the small air-bladder of these fishes: they also lodge the little ossicles which bring this vertebral tympanum into communication with the prolongations or *atria* of the labyrinth*.

In a large South American siluroid fish (*ib.* figs. 3 and 4), I found the fore-part of the vertebral column of the trunk apparently formed by one large vertebra, the body of which sent a broad triangular plate outwards on each side, giving it a rhomboidal figure, viewed from below: these plates in this fish support and coalesce with five parapophyses (*p*, 5, 4, 3, 2, *a*), which ascend and increase in breadth as they approach the skull, where they join the paroccipitals (*p o*), as they are, themselves, joined together so as to form a continuous broad oblique outstanding plate of bone. Above these, the continuous bony neural arch is perforated for the exit of five pairs of nerves; the dorsal and ventral roots escaping separately, as in the sacrum of birds (fig. 3, *n* 2, *n*, 5). The coalesced neural spines send up a lofty pointed plate to the overhanging supraoccipital. On vertically bisecting this specimen, I found the central parts of the bodies of five vertebræ (*c*, *a*, 2, 3, 4, 5) which had been developed in the notochord, distinctly marked out, and preserving in their anterior and posterior deep concavities the persistent gelatinous remains of the notochord; although the rest of the circumference of such centrums were anchylosed to the cortical or peripheral parts developed from the capsule of the notochord, viz. to the continuous expanded plate of bone (*c e*) below, to the parapophyses laterally, and to the neurapophyses above. The body of the first vertebra, or atlas (*c a*), presented the exception of being quite detached from its elevated parapophyses, as well as from its neural arch; it was anchylosed only to the bony plate below. The body of the second vertebra was six times as long as that of the atlas: yet the apices of the two deep terminal jelly-filled cones extended to and met in its centre. The bodies of the third and fourth vertebræ were elongated, but less so than that of the axis: the body of the fifth vertebra (*c* 5) was singularly modified; its anterior half presenting the long and slender character of the antecedent vertebræ; whilst the posterior half was suddenly shortened, but extended in depth and breadth so as to adapt its shallow posterior concavity to that of the short and broad body of the first free vertebra of the trunk, which is followed by others of similar character. I have seen few more remarkable instances of adherence to type, irrespective of obvious function, than the persistence of the biconcave articular cavities, with the elastic capsules and contained fluid, in the centrums of these five rigidly fixed anterior vertebræ of the siluroid fish.

The continuous bony plate supporting those centrums was perforated lengthwise by the aorta, offering another mode of formation of a hæmal canal (*c h*), viz. by exogenous ossification in and from the lower part of the outer layer of the capsule of the notochord: the carotid hæmal canal in the necks of birds seems to be similarly formed; and the neck of the ichthyosaurus derives additional strength and fixation from apparently detached developments of bone in the lower part of the capsule of the notochord, at the inferior interspace between the occiput and atlas, and at those of two or three succeeding cervical vertebræ †.

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* Weber, G. H., De Aure et Auditu Hominis et Animalium, 4to. 1820.

† Sir Philip de M. Grey Egerton, in Geol. Trans. 2nd ser. vol. v. p. 187, pl. 14.

The so-called 'body of the atlas' in recent saurians, birds, mammals and man, is the homologue of the first of these subvertebral wedge-bones, and represents only the inferior cortical part of such body. The odontoid process of the axis is the central and main part of the body of the atlas. It cannot be the anterior articular epiphysis of the second vertebra, since this is represented by a distinct centre of ossification between the odontoid process and the body of that vertebra, according to Professor Müller's observation in a fœtal foal*, and the odontoid exists in birds and reptiles in which the bodies of the vertebræ have no terminal epiphyses as in young mammals.

The diverging appendages of the hæmal arch in the abdominal vertebræ of fishes present the form of long and slender spines (fig. 17, *a a*), usually attached to, or near the head of the ribs, and extending upwards, outwards and backwards, between the dorsal and lateral portions of the muscular segments, to which they afford a firmer fulcrum or basis of attachment; acting, therefore, as so many pairs of rudimental and concealed limbs. They are termed the 'obere rippe' by Meckel, and at the fore-part of the abdomen of the polypterus they are stronger than the pleurapophyses themselves. As the vertebræ approach the tail these appendages are often transferred gradually, from the pleurapophysis to the parapophysis, or even to the centrum and neural arch.

In the air-breathing vertebrata, in which the heart and breathing organs are transferred backwards to the trunk, the corresponding osseous segments of the skeleton are in most instances developed to their typical completeness, in order to encompass and protect those organs. The thoracic hæmapophyses in the crocodiles are partially ossified, and in birds (fig. 15, *h*, *h*) completely so; in which class the hæmal spines of the thorax (*hs*) coalesce together, become much expanded laterally, and usually develope a median crest downwards to increase the surface of attachment for the great muscles of flight. This speciality is indicated by the name 'sternum' applied to the confluent elements in question. The abdominal hæmapophyses and spines retain their primitive aponeurotic condition, though still preserving their characteristic expansion †. In the crocodiles and enaliosaurs the abdominal hæmapophyses are also ossified; and, in the latter, they manifest the same composite character which has been noticed in the pleurapophyses of the sturgeon, consisting of three or more pieces, which overlap each other ‡. The abdominal hæmal spines, in the *Plesiosaurus Hawkinsii*, are transversely extended, they are marked *a*, *c* in the figure quoted below: the compound hæmapophyses themselves are marked *b b* in the same figure.

The typical thoracic vertebræ of birds support diverging appendages (fig. 15, *a*, *a*), either anchylosed as in most, or articulated as in the penguin and apteryx, to the posterior border of the pleurapophysis (*pl*). The function of the appendages in this form of typical vertebra is to connect one hæmal arch with the next in succession, so as to associate the two in action, and to give firmness and strength to the whole thoracic cage. (A portion of the next rib so overlapped is shown at *pl*, *a*, fig. 15.)

With regard to the connections of the pleurapophyses, we have seen that, in fishes, they may be directly attached to the centrum, or to the ends of the parapophyses (fig. 17, *p*), or they may be quite detached from their proper segment, and suspended to the hæmal arch of another vertebra, as in the case of the clavicle (fig. 25, *ss'*). In batrachians, ophidians, and lacertians, the proximal end of the pleurapophysis is simple, as in fishes, but is articulated to an exogenous tubercle or transverse process from the side of the centrum or from the base of the neural arch, called 'diapophysis,' which is a distinct part from the autogenous parapophyses in fishes. The anterior vertebræ of crocodiles have an exogenous inferior transverse process from the side of the centrum, answering to the 'parapophysis,' as well as a superior transverse process or 'diapophysis' developed from the base of the neurapophysis: and the proximal end of the pleurapophysis bifurcates and articulates with both transverse processes, circumscribing with them a foramen at the side of the centrum. A similar structure obtains in the cervical and anterior thoracic vertebræ of birds and mammals: thus the rib (*pl*) in fig. 15 articulates with the parapophysis *p* and the diapophysis *d*. Very few, however, of the thoracic ribs in the cetaceans offer this structure; the first or second rib may reach the centrum, but the rest are appended to the ends of the long diapophyses, and a character of affinity to the saurians is thus manifested. The cervical region is distinguished by the shortness of the pleurapophyses and the absence of bony hæmapophyses, in saurians, birds, and mammals; but in the warm-blooded classes the short floating vertebral ribs soon anchylose to the diapophyses and parapophyses, and constitute thereby the 'anterior roots of the perforated transverse process' of anthropotomy[*]. The cervical pleurapophyses are indicated diagrammatically at *pl*, in the neck of the embryo skeleton (fig. 25): those of the seventh cervical vertebræ sometimes attain in the human subject proportions which acquire for them the name of 'ribs.' The pleurapophyses retain their moveable articulation in the ninth, and sometimes the eighth, vertebræ of the elongated neck of the three-toed sloths[†].

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* Vergleichende Anatomie der Myxinoiden. Abhand. Akad. der Wissensch. Berlin, 1834, p. 106.

† Myology of Apteryx, Zool. Trans., vol. iii. pt. iv. pl. 28, f^5, f^6.

‡ Buckland, Bridgewater Treatise, vol. ii. pl. 18, fig. 3.

The thoracic or dorsal vertebræ of mammalia are characterized by the free articulations of the pleurapophyses (fig. 25, *pl*): most of these are much elongated, and most, if not all, support hæmapophyses (ib, *h*); which, in a greater or less number of the anterior vertebræ, articulate with hæmal spines (ib. *hs*), completing the arch; these spines commonly remain distinct, and are called, some 'sternebers,' others 'manubrium,' and 'xiphoid appendage,' and together they constitute the 'sternum.' In most mammals the thoracic hæmapophyses are cartilaginous: they become ossified in *Dasypus*, *Myrmecophaga*, the megatherioids and monotremes. The hinder pleurapophyses, which progressively diminish in length, also, usually become simply suspended to the diapophyses; all the ribs are so attached in *Balæna longimana*, according to Rudolphi. The lumbar vertebræ, which in some mammals show, in the fœtal state, distinct rudiments of pleurapophyses more minute than those in the neck, have them soon anchylosed to the extremities of the diapophyses, which are thus elongated; and the vertebra is characterized in anthropotomy as 'having no ribs, but simple imperforate transverse processes.' The hæmapophyses of these segments of the skeleton are represented by the 'inscriptiones tendineæ' (fig. 25, *h''*); they do not advance even to the state of cartilage, but retain the primitive condition which they presented in the corresponding part of the trunk in fishes.

If a vertebra succeeding the lumbar or abdominal ones have its hæmal arch completed, as in the thorax, by pleurapophyses and hæmapophyses, with diverging appendages, forming the 'pelvic arch and hind or lower limbs (fig. 28, D', H, A),' it is called a 'sacrum'. If two or more vertebræ anchylose together, without such completion of the typical character, they likewise are said to form a 'sacrum,' of which an example may be found in

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[*] Meckel, Archiv für Physiologie, B. i. (1815) p. 594, pl. vi. fig. 12, *e*; and System der Vergleichend. Anatomie, B. ii. p. 294.

[†] Prof. Th. Bell. Trans. Zool. Society, i. p. 115. pl. 116. *a*, *b*.

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Summary of modifications of corporal vertebræ.—To sum up the kind and degree of modification to which the several elements of the primary segments of the endoskeleton of the trunk are subject, without masking their general homology, we may commence with the *centrum*; and first, as to its existence It is wanting, as an ossified part, in the atlas of the wombat and koala[*], in which it remains permanently cartilaginous: in the petaurists, kangaroos, and potoroos, ossification extends from the bases of the neurapophyses into this cartilage, but the neural arch or ring long remains interrupted by a median fissure below. In man the rudimental body of the atlas is sometimes ossified from two or even three distinct centres[†]. The centrums at the opposite extremity of the vertebral column in homocercal fishes are rendered by centripetal shortening and bony confluence fewer in number than the persistent neural and hæmal arches of that part. The centrums do not pass beyond the primitive stage of the notochord in the existing lepidosiren, and they retained the like rudimental state in every fish whose remains have been found in strata earlier than the permian æra in Geology, though the number of vertebræ is frequently indicated in Devonian and Silurian ichthyolites by the fossilized neur- and hæm-apophyses and their spines[‡]. The individuality of the centrums is sometimes lost by their mutual coalescence without shortening.

Although the normal form of the centrum is cylindrical, it may be cubical, conical, hour-glass shaped, like a longitudinal bar, like a transverse bar, like a depressed or a compressed plate, like a ploughshare, &c. The co-adapted terminal surfaces of the centrum may be flat, slightly concave, deeply concave, cupped or conical, concave vertically and convex transversely at one end and the reverse at the other end[§]; or the fore-end may be concave and the hind-end convex[‖]; or the reverse[¶]; or both ends may be convex[**]; or both ends produced into long pointed processes with intervening deep fissures, so as to interlock together by a deeply dentated sutural surface[††].

The centrum may be quite detached from its neural arch (atlas of siluroid and many fishes), and from its hæmal arch (atlas of most fishes).

The centrum may develope not only parapophyses but inferior median exogenous processes, either single, like those of the cervical vertebræ of saurians and ophidians (which in *Deirodon scaber* perforate the œsophagus, are capped by dentine, and serve as teeth[‡‡]); or double (atlas of *Sudis gigas*[§§] and the lower cervical vertebræ of many birds); or the fibrous sheath of the notochord may develope a continuous plate of bone beneath two or more nuclei of centrums, formed by independent ossification in the body of the notochord; these nuclei being partially coherent to the peripheral or cortical plate. The vertebral centrum often shows the principle of vegetative repetition by its partial ossification in the form of two or three bony rings, which answer to a single neural arch (*Heptanchus*[‖‖]); or by three osseous discs, one for each articular surface, and a thicker intermediate piece, as in all fœtal mammals, and throughout life in some cetaceans.

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[*] Art. Marsupialia, Cyclopædia of Anatomy and Physiology, vol. iii. p. 277, fig. 99.

[†] Meckel, Archiv für Physiol. i. taf. vi. fig. 1.

[‡] See the admirable Monograph by Agassiz, Sur les Poissons Fossiles du Système Dévonien, 4to, 1846.

[§] Most birds.

[‖] Existing saurians and ophidians.

[¶] Extinct saurian called '*Streptospondylus*;' existing *Salamandra*, *Lepidosteus*.

[**] 4th cervical of *Emys*, Bojanus, Anat. Test. Europ., tab. xiv. fig. 51, 4. 1st caudal of crocodile.

[††] Cervicals or anterior trunk-vertebræ of *Fistularia*.

[‡‡] Jourdan, cited in Cuvier's Leçons d'Anat. Comparée, ed. 1835, p. 340, and 'Odontography,' p. 179.

[§§] Agassiz in Spix, Pisces Brasilienses, 4to, 1829, p. 6, tab. B, fig. 8.

[‖‖] Müller and Agassiz, in Recherches sur les Poissons Fossiles, t. iii. tab. 40*, fig. 1.

With respect to function, the centrum forms the axis of the vertebral column, and commonly the central bond of union of the peripheral elements of the vertebra: as a general rule it supports, either immediately or through the medium of the approximated or conjoined bases of the neurapophyses, the neural axis (in the trunk called myelon, or spinal marrow, and its membranes); the terminal centrums being usually deprived of this function by the withdrawal of that axis from them in the course of its centripetal or concentrative movement.

The *neurapophyses* are more constant as osseous or cartilaginous elements of the vertebræ than the centrums; but they are absent, under both histological conditions, at the end of the tail in most air-breathing vertebrates, where the segments are reduced to their central elements. The neurapophyses lose their primitive individuality by various kinds and degrees of confluence; as *e. g.* first, of the bases of each pair with their supporting centrum; secondly, of the apices of each pair with one another and with the neural spine,—the lepidosiren affording a rare exception of the persistent individuality of this element and of each neurapophysis throughout the trunk; thirdly, of two or more neural arches with one another, as in the neck of some fishes, cetacea, and armadillos, and in the sacrum of birds and mammals; where they also often coalesce with the pleurapophyses, as they do in the neck of most mammals and birds. The neurapophyses rarely depart from the form of plates, either broad or high, or both; sometimes they are straight, sometimes arched, sometimes bent; sometimes by the inward extension of their bases, they form together a bony ring above the centrum, excluding both that and the spine from the neural canal. The neurapophyses may develope, as exogenous processes, either diapophyses or zygapophyses, and the latter are sometimes double from both the anterior and posterior borders of the plates; as *e. g.* in the vertebræ of *Mugil*, in some serpents, and in the lumbar vertebræ of some mammals. The observed extent of variation of position of the neurapophyses is from the upper surface of their own centrum to above the next intervertebral space, so as to rest equally on two centrums; or they may be uplifted bodily from their centrum, and wedged or suspended between the two contiguous neural arches, as *e. g.* in the atlas of ephippus and other deep-bodied fishes.

Except in the cartilaginous neurapophyses of the sturgeon, I am not aware of any instance of the subdivision of this element into two pieces, placed vertically upon each other. Some plagiostomes show the principle of vegetative repetition in two or three star-like centres of ossification, side by side, in the primitive basis of the neurapophysis, but the second of the two cartilaginous plates on each side of the neural canal, coextensive with the single centrum, in most sharks, which second piece has the form of a wedge with the small end directed down over the intervertebral space, seems to answer, as Prof. Müller has suggested, to the intercalary or interneural piece in bony fishes.

The most constant functional relation of the neurapophysis is to protect the spinal nerve in its exit from the spinal canal, either by a direct perforation of the neurapophysis (many fishes, and some mammals), by a notch in the margin, or by the interspace between two neurapophyses. This function alone is performed, in reference to the nervous system, at the posterior part of the vertebral column in many animals, where the place of the shortened myelon is occupied by the lengthened roots of the nerves: in the rest of the trunk the neurapophyses protect also the neural axis. The original relation of each neurapophysis to the segments of that axis is determined by the place of connection of the perforating nerve with the shortened myelon.

The *neural spine* commonly retains in the trunk the form indicated by its name; but in the atlas of the crocodile, where it is distinct from the neurapophyses, it is a depressed plate. In the thorax and abdomen of chelonians it becomes still more expanded and flattened, and its borders unite by dentated suture to contiguous spines and to the similarly expanded pleurapophyses. The neural spine is absent in the thin annular cervicals of the mole; it is unusually developed and forms a thick square columnar mass of bone in the cervicals of the opossum. It is double in the anterior vertebræ of some fishes: in the barbel one stands before the other; in the tetrodon they stand side by side: and various other minor modifications of this peripheral element might be cited.

The *parapophyses* of the trunk-vertebræ manifest their autogenous character in fishes alone; and in most species the character is soon lost, the parapophyses becoming confluent with the centrum; and, in the tail, either with the pleurapophyses also, or with each other and the hæmal spine, thus completing the hæmal canal (fig. 16). Amongst air-breathing vertebrates the parapophyses of the trunk-segments are present only in those species in which the septum of the heart's ventricles is complete and imperforate, and here they are exogenous and confined to the cervical and anterior thoracic vertebræ, or to the sacrum (as in the ostrich, figs. 15 and 27, *p*). The parapophyses are subject to a certain extent of variation as to form: they are either mere tubercles; or simple, shorter or longer, transverse processes; or they may take the form of long plicated laminæ (in the tails of some pleuronectidæ): they are longer and broader than the pleurapophyses in the cod-tribe; and are sometimes much expanded in the anterior vertebræ of fishes, where they ascend in position, and in the siluroid species above described, coalesce to form a broad outstanding ridge, directed outwards and a little upwards, and rising as they approach the cranium, where they are joined by close suture to the paroccipitals.

The normal function of the parapophyses is to give attachment to muscles and articulation to ribs, and, occasionally, additional strength and fixation to anchylosed portions of the vertebral column. As a rare and exceptional instance, the expanded and excavated parapophyses of the second and third vertebræ in the genus *Cobitis* perform an office closely analogous to one of those of the mastoid in man, since they inclose air-cells brought into communication with the acoustic labyrinth by a chain of small ossicles: and these singularly modified rudiments of the swim-bladder seem to have no other function in the groveling loaches than that in connection with the sense of hearing.

The *pleurapophyses* are less constant elements than the neurapophyses; they exist as free appendages or 'floating vertebral ribs' in the trunk, and sometimes at the fore-part of the tail, in fishes, serpents, and certain batrachians (fig. 28, *pl*). The atlas has its pleurapophyses in most fishes, but they are often detached from their centrum, and sometimes joined to long bony hæmapophyses, as is well-seen in the *Argyreiosus*, and other deep-bodied scomberoids. Ossified hæmapophyses are not present in any other vertebræ of the trunk in fishes. In batrachians the pleurapophyses of the single pelvic vertebra are similarly connected with hæmapophyses, and the costal arch is there completed. In the menopome, the pleurapophysial element of the sacrum, *ib. pl'*, is ossified from two centres. Such typical vertebræ are more common in the higher air-breathing classes. Here the pleurapophyses have generally the long and slender form understood by the word 'rib;' but they expand into broad plates in the thorax of the apteryx, in the anterior thoracic vertebra of whales, and more especially in the carapace of chelonians, where they are joined to each other by suture, and also to the expanded neural spines. These broad pleurapophyses are occasionally ossified from two centres in the great land-tortoises of India and the Galapagos isles. The free extremities of the short cervical pleurapophyses of crocodiles and plesiosaurs are expanded and produced forwards and backwards, like axe-blades, whence the name of 'hatchet-bones,' applied to them prior to the recognition of their true homology.

The pleurapophyses are appended sometimes simply to the ends of parapophyses; sometimes to the ends of diapophyses; sometimes by a head and tubercle to both kinds of transverse processes; sometimes directly to the side of the centrum; and sometimes they are shifted backwards over the intervertebral space, and are articulated equally to two centrums (human thorax), and sometimes to two centrums, to a neurapophysis and to a long diapophysis, as in the sacrum of the ostrich (fig. 27, *pl*). In the atlas of some fishes the pleurapophysis is detached from its centrum, and is suspended, with its hæmapophysis, from the antecedent hæmal arch (scapulo-coracoid). In some sturgeons the abdominal pleurapophyses are composed of two or more cartilaginous pieces. I have observed some of the expanded pleurapophyses in the great *Testudo elephantopus* ossified from two centres, and the resulting divisions continuing distinct but united by suture. The pelvic pleurapophysis is in two pieces, as a general rule (fig. 28, *pl′* attached to D′); and the lower piece is the seat of that most common and simple kind of modification, viz. increase of size with change of form from the cylindrical to a flat bone (as indicated by the dotted line in fig. 27), whereby it comes into connection with the pleurapophyses of other vertebræ besides the proximal piece of its own; such pleurapophyses having their development stunted so as not to exceed in size the proximal portion of the pelvic pleurapophysis, whose expanded distal portion (*es*) receives the special name of 'ilium.' This bone retains its rib-like shape however in the chelonians, as in the batrachians: in most species it unites below with two hæmapophyses, called, on account of their modifications of form and proportions, 'ischium' and 'pubis.' The pleurapophyses defend the hæmal or visceral cavity; they are the fulcra of the moving powers which expand and contract such cavity in respiration, when its walls admit of those movements; they frequently support 'diverging appendages,' and give origin to muscles moving such appendages, or acting upon the vertebral column. In some exceptional cases the pleurapophyses become, themselves, locomotive organs, as in serpents and the *Draco volans*.

The *hæmapophyses*, as osseous elements of a vertebra, are less constant than the pleurapophyses; although they sometimes exist in segments, *e. g.* the lumbar vertebræ of certain saurians, and in the case of the ischium, or second pelvic hæmapophysis, in which the corresponding pleurapophyses are absent, or short, or anchylosed to the transverse processes. The only true bony hæmapophyses in the trunk of fishes appear to be those of the atlas, forming the lower piece of the epicoracoid; and of the last (?) abdominal vertebra, forming the ischial or pubic inverted arch supporting the appendages called 'ventral fins.' It is at least to the last abdominal vertebra solely that the homologous arch and appendages are connected, by the medium of the pleurapophyses (iliac bones) in the batrachians, and it needs but the removal of the pleurapophysis, or of its second complementary portion (*pl′* in fig. 28), to reduce that vertebral segment to the condition which it presents in an abdominal fish. The so liberated inferior (hæmapophysial) portion of the pelvic (last abdominal costal) arch is subject, in fishes, to changes of position far more extensive than have been observed in the neurapophyses or pleurapophyses of the trunk-vertebræ, without however preventing the recognition of the segment to which such shifted hæmapophyses actually and essentially belong. The homologous hæmal arch exists in the same free and detached condition in cetaceans and enaliosaurs; but in all other air-breathing vertebrates it is connected with the iliac bones and completes the typical character of the proper sacral vertebra. The bony hæmapophyses of the lumbar vertebræ are found suspended in the fleshy abdominal walls of certain saurians: but in the region of the thorax in these and higher vertebrates, the hæmapophysis (fig 15, *h*) articulates by one end to the pleurapophysis (*pl*) and by the other to the hæmal spine (sternal bone, *hs*); or its lower end is attached to a contiguous hæmapophysis; or it is suspended freely from the pleurapophyses (as in the 'floating ribs' of man and mammals), or it may be joined below to the sternum, and have its upper end free, as in the seventh dorsal vertebra of the *Ciconia Argala*. When the upper end of the hæmapophysis articulates with the pleurapophysis in birds, it is usually by a distinct condyloid joint, with smooth articular cartilage and a synovial capsule.

Where hæmapophyses exist in the tail, they articulate directly to the under part of the centrum, or to two centrums at the intervertebral space; and are either free at the opposite end, as in some caudal vertebræ of serpents and in those of the enaliosaurs, or they are confluent with each other at their distal ends; when each pair of hæmapophyses forms the so-called V-shaped or chevron-bone. The changes of position of that detached 'pubic arch' or 'chevron-bone' which supports the ventral fins in fishes afforded Linnæus the characters of the orders 'Abdominales,' 'Thoracici,' and 'Jugulares' in the 'Systema Naturæ'; and its immortal author, in giving the name 'Apodes' to those fishes in which the ventral fins were absent, concisely indicates his perception of their relation to the hind-legs of batrachia and the lower limbs of man. If, then, mere change of relative position, however extensive, failed to conceal the special homology of the detached portion of the pelvic arch and its appendages from the keen-sighted naturalist, still less ought such a character to blind the philosophic anatomist to the general homology of such detached vertebral elements, or prevent his tracing them, wherever he may find them, to the remainder of their proper segment; especially when its place is so clearly and beautifully indicated, as it is by the condition of the pelvic arch in the perennibranchiate reptiles (fig. 28).

The function of the hæmapophyses is to complete, with or without a hæmal spine, the hæmal arch of the vertebral segment; and, in so far to protect the hæmal or visceral cavities and support their contents. They give attachment to the lower or ventral portions of the primary muscular segments 'myocommata'[*], called 'intercostals' in the thorax, and 'recti abdominis' in the abdomen of the higher vertebrata; and they thus serve as fulcra to the muscles that expand and contract the abdominal or thoracic-abdominal cavity: and sometimes more directly aid in these movements by the elasticity resulting from an arrest in their histological development at the cartilaginous stage, *e.g.* in the thorax of most mammals. Hæmapophyses may support or aid in supporting diverging appendages; and in giving attachment to the muscles of those appendages. The hæmapophyses are usually slender, simple bones, varying in length: they are broad, flat, and overlap each other in the thorax of monotremes: they become broader and shorter in the expanded and fixed thoracic abdominal bony case of chelonians, and are still broader where they close the pelvic arch in the plesiosaurs. In the abdominal region of these extinct saurians and in crocodiles, the freely suspended hæmapophyses are compounded of two or more overlapping bony pieces.

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[*] See the description of these segments, usually confounded under the name of the 'great lateral muscle' or 'longitudinal muscles' in fishes.—Hunterian Lectures on Vertebrata, 8vo, pp. 163–165.

The *hæmal spine* is much less constant as to its existence, and is subject to a much greater range of variety, when present, than is its vertical homotype above, which completes the neural arch. Long, slender, and 'spinous' in the tail, the hæmal spine is reduced to a short and thick bone, often flattened, in the thorax of mammals, a series of thirteen such modified spines forming the so-called 'sternum' in the two-toed sloth: the thoracic hæmal spines are few in number, and are expanded and perforated in the whales: the horizontal extension of this vertebral element is sometimes accompanied by a median division, or in other words, it is ossified from two lateral centres; this is seen in the development of parts of the human sternum: the same vegetative character is constant in the broader thoracic hæmal spines of birds; though, sometimes, as *e. g.* in the struthionidæ, ossification extends from the same lateral centre lengthwise, *i. e.* forwards and backwards, calcifying the connate cartilaginous homologues of halves of four or five hæmal spines, before these finally coalesce with their fellows at the median line. In some other birds, however, there are two or more lateral centres, and usually, also, a median one, from which the ossification of the keel extends downwards, prior to its confluence with the rest of the 'sternum.' In the thorax of chelonians four hæmal spines are established, each by two lateral centres of ossification, forming four pairs of sternal bones with a ninth 'entosternal' piece between the first and second pairs. The 'plastron' is the result of this extreme development of the hæmal spines:—the modified moieties of which, remaining permanently distinct and united by suture, have received from Geoffroy St. Hilaire* the convenient special names of 'episternals,' 'hyosternals,' 'hyposternals' and 'xiphisternals,' respectively, as they succeed each other from before backwards.

The *diverging appendages* are, as might be expected, of all the elements of the vertebral segment, the least constant in regard to their existence, and the subjects of the greatest amount and variety of modification. Simple slender spines or styles in fishes (fig. 17, *a a*), simple plates retaining long their cartilaginous condition in crocodiles, short flat slightly curved pieces in birds (fig. 15, *a a*), in some of the lowest species of which, *e. g. Aptenodytes*, they become expanded, like their homologues in the crocodile; such, with one exception, is the range of the variety of form to which these parts are subject in the segments of the trunk. But that exception is a remarkable one: even under its normal ichthyic condition, as a simple style or filament, the diverging appendage of the insulated hæmapophysial portion of the pelvic arch in the protopterus† and lepidosiren‡ is composed of many cartilaginous segments, and projects freely from the surface, carrying with it a smooth covering of integument. In other fishes similar filaments or jointed rays are progressively added to the sustaining arch, which cause a progressive expansion of the common investing fold of skin, forming the organ called the 'ventral fin,' which is accordingly described by the ichthyologist as having two rays (*Blennius*), three rays (*Zoarces*), up to more than twenty rays, (as *Acipenser* in the sturgeons).

When we quit the piscine class we find the diverging appendage of the pel-

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* Du Sternum considerée dans les Oiseaux et dans les Poissons. Anatomie Philosophique, p. 69. pl. 2, fig. 21. Here Geoffroy contends that the parts of the hyoid arch (39, 40 and 43) are the homologues of the modified hæmal spines which he calls episternals, hyosternals and hyposternals in the plastron of the turtle: but these names may well be retained, that of 'hyosternal' being used in an arbitrary sense, without reference to the hypothesis which first suggested it.

† Linn. Trans. vol. xviii. pl. 23, fig. 4, *s*. Lectures on Vertebrata, p. 79, figs. 27, 66.

‡ Bischoff, op. cit. pl. 2, fig. 5, *e*.

vic arch resuming its primitive unity, and with fewer joints than in lepidosiren, but manifesting the principle of vegetative repetition by a bifurcation of the distal segments. Such is its form in the *Proteus anguinus* and in the *Amphiuma didactylum*: in another species of amphiume, the radiated type is more strongly marked by the subdivision of the last segment into three rays, the homology of which with certain of the five terminal rays, called toes or digits in the human foot, is signified by Cuvier's specific name 'tridactylum' applied to this species; the middle segment of the appendage is bifid, the first one is undivided. In the menopome (fig. 28), the proximal segment (65) is likewise single, the second segment (66, 67) double, and a mass of cartilage (68) separates this from the last segment which branches into five jointed rays (69). In the frog two styliform bones are developed in the position of the cartilage (68 in fig. 27), forming a fourth segment of the division: they are replaced by more numerous and shorter bones in higher vertebrates, in which it will be unnecessary to pursue the metamorphoses of the appendage as it is adapted for swimming, steering, balancing and anchoring, for exploration, for burrowing, creeping, walking and running, for leaping, seizing, climbing, or sustaining erect the entire frame of the animal. Its parts under these endless and extreme modifications have necessarily received special names: the first segment (65) is the thigh, *femur*; the second is the leg, and its two rays or bones are called *tibia* (66) and *fibula* (67): the segment (68) is called ankle or *tarsus*, each of its component ossicles having its proper name; and the last radiated segment (69) includes the metatarsus and phalanges: the segments 68 and 69 are termed collectively, the foot, *pes**.

The primitive function of the simple diverging appendages (fig. 17, *a*, *a*) of the abdominal vertebræ in fishes is closely analogous to that of the more developed appendage of the pelvic vertebra, viz. to aid in locomotion, as fulcra to the muscles concerned in that act. In crocodiles and birds they serve to connect one costal arch with the next arch in succession, associating them in action or giving fixity and strength to the whole thoracic cage.

Any given appendage might, however, have been the seat of such developments as convert that of the pelvic arch into a locomotive limb: and the true insight into the general homology of limbs leads us to recognise many potential pairs in the typical endo-skeleton. The possible and conceivable modifications of the vertebrate archetype are far from having been exhausted in the forms that have hitherto been recognised, from the primæval fishes of the palæozoic ocean of this planet up to the present time.

The beneficent Author of all, who has created other revolving orbs, with relations to the central source of heat and light like our own, may have willed that these also should be the seat of sentient beings, suited to all the conditions of animal enjoyment existing in such planets; basking, perhaps, in the solar beams by day, or disporting in the soft reflected light of their earth's satellites by night. The eyes of such creatures, the laws of light being the same, would doubtless be organized on the same dioptric principles as ours; and, if the vertebral column should there, as here, have been adopted as the basis of the higher animal forms, it may be subject to modifications issuing in forms such as this planet has never witnessed, and which can only be conceived by him who has penetrated the mystery of the vertebrate archetype, and recognised the kind and mode and extent of its modifications here.

It is, for example, by no means essential to that organic type that it should be 'tetrapodal': although it best accords with the force of attraction and other

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* A remarkable example of the extent to which an early or low form of such segment may be regained by abnormal development in a higher species is given by Kerkringius, Opera Omnia, 4to. 1717, p. 55, tab. viii.

conditions of our globe, that not more than two pairs of the latent limbs or appendages of the vertebral segments should be developed to react, as locomotive instruments, upon its waters, its atmosphere and its dry land.

The views of the essential relations of such limbs to the vertebrate type which suggest these and similar reflections, may not be accepted by all anatomists: some may be disposed to regard the parts 63 and 64 in fig. 28 as peculiar superadditions, rather than a reappearance of normal elements completing the costal or hæmal arch of a segment of the endo-skeleton and restoring it to its typical condition: and, in the same spirit, they may deny the special homology of the radiated appendage A, with the hinder filamentous fin of the lepidosiren, and the ventral fins of other fishes, and consequently, will repudiate its general homology as the diverging appendage of such hæmal arch, and its serial homology with the simple diverging appendages of the thoracic-abdominal vertebræ of fishes, crocodiles and birds.

I am sensible how large a demand is made on the most philosophic faith in general laws of organization, by seeking acquiescence in the view of the parts of the hind-limb, so variously and definitely modified for special functions, as being the homologues of segments and rays, which are the result in the first instance of the common course of vegetative repetition of a single vertebral element—an element under all circumstances compounded teleologically, and, therefore, essentially representing or equivalent to one bone.

But here I must explain what I mean by 'teleological composition.' Individual parts of a skeleton,—what are commonly called 'bones,'—are frequently 'compound' or composed of the coalescence of several primarily distinct osseous pieces. In human anatomy every single and distinct mass of osseous matter entering into the composition of the adult skeleton is called 'a bone'; and Soemmerring, who includes the thirty-two teeth in his enumeration, reckons up from 259 to 264 such bones. He counts the os spheno-occipitale as a single bone, and also regards, with previous anthropotomists, the os temporis, the os sacrum, and the os innominatum, as individual bones; the sternum, he says, may include two or three bones, &c*. But in birds the os occipitale is not only anchylosed to the sphenoid, but they both very soon coalesce with the parietals and frontals; and, in short, the entire cranium proper consists, according to the above definition, of a single bone. Blumenbach, however, applying the human standard, describes it as composed of the proper bones of the cranium consolidated, as it were, into a single piece†. And in the same spirit most modern anthropotomists, influenced by the comparatively late period at which the sphenoid becomes anchylosed to the occipital in man, regard them as two essentially distinct bones. In directing our survey downwards in the mammalian scale, we speedily meet with examples of persistent divisions of bones which are single in man. Thus it is rare to find the basioccipital confluent with the basisphenoid in mammalian quadrupeds; and before we quit that class we meet with adults in some of the marsupial and monotrematous species, for example, in which the supraoccipital, 'pars occipitalis proprie sic dicta,' of Soemmerring, is distinct from the condyloid parts, and these from the basilar or cuneiform process of the os occipitis: in short, the single occipital bone in man is four bones in the opossum or echidna; and just as the human cranial bones lose their individuality in the bird, so do those of the marsupial lose their individuality in the ordinary mammalian and human skull. In many mammals we find the pterygoid processes of anthropotomy permanently distinct bones; even in birds, where the progress of ossific confluence is so general and rapid, the pterygoids and tympanics, which are subordinate processes of other bones in man, are always independent bones.

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* De Corporis Humani Fabricâ, t. i. p. 6.

† Manual of Comparative Anatomy, by Lawrence, ed. 1827, p. 56.

In many mammals, the styloid, the auditory, the petrous, and the mastoid processes remain distinct from the squamous plate of the temporal, throughout life; and some of these claim the more to be regarded as distinct bones, since they obviously belong to different natural groups of bones in the skeleton; as the styloid process, for example, to the series of bones forming the hyoidean arch.

The artificial character of the anthropotomical view of the os sacrum, in which that more or less confluent congeries of modified neural arches is counted as a single component bone of the skeleton, is sufficiently obvious. The os innominatum is represented throughout life in most reptiles by three distinct bones, answering to the iliac, ischial, and pubic portions in anthropotomy. The sternum in most quadrupeds consists of one more bone than the number of pairs of ribs which join it; thus it includes as many as thirteen distinct bones in the *Bradypus didactylus*.

The arbitrary character of the definition of a bone, as 'any single piece of osseous matter entering into the composition of the adult skeleton,' the complex nature of many of such single bones, and the essential individuality of some of the processes of bone in anthropotomy, are taught by anatomy properly so called, which reveals the true natural groups of bones, and the modifications of these which peculiarly characterise the human subject.

It will occur to those who have studied human osteogeny, that the parts of the single bones of anthropotomy which have been adduced as continuing permanently distinct in lower animals, are originally distinct in the human fœtus: the occipital bone, for example, is ossified from four separate centres; the pterygoid processes have distinct centres of ossification; the styloid, and the mastoid processes, and the tympanic ring, are separate parts in the fœtus. The constituent vertebræ of the sacrum remain longer distinct; and the ilium, ischium, and pubes are still later in anchylosing together, to form the 'nameless bone.'

These and the like correspondences between the points of ossification of the human fœtal skeleton, and the separate bones of the adult skeletons of inferior animals, are pregnant with interest, and rank among the most striking illustrations of unity of plan in the vertebrate organization.

The multiplication of centres from which the ossification of an ultimately single bone often proceeds has especially attracted the attention of the philosophical anatomists of the present century with reference to the right or natural determination of the number of the constituent parts of the vertebrate skeleton. Geoffroy St. Hilaire, in his memoir on the skull of birds, in 1807, says, "Ayant imaginé de compter autant d'os qu'il y a de centres d'ossification distincts, et ayant essayé de suite cette manière de faire, j'ai eu lieu d'apprécier la justesse de cette idée[*]." Cuvier adopted and retained the same idea to the last. Commenting in the posthumous edition of the 'Leçons d'Anatomie Comparée[†]' on the character of some of the definitions of single bones in anthropotomy, he, also, concludes that, in order to ascertain the true number of bones in each species, we must descend to the primitive osseous centres as they are manifested in the fœtus. But according to this rule we should count the humerus as three bones and the femur as four bones, in the human skeleton; for the ossification of the thigh-bone begins at four distinct points, one for the shaft, one for the head, one for the great trochanter, and one for the distal condyles: such deference, however, to the judgment of the great Comparative Anatomist has been withheld by the most devoted of his admirers; whose disinclination to regard these parts and processes as distinct bones is justified by the fact that in birds and reptiles the femur is developed from a single centre.

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[*] Annales du Muséum, t. x. p. 344.

[†] Tom. i. 1835, p. 120. "Mais ces distinctions sont arbitraires, et pour avoir le véritable nombre des os de chaque espèce, il faut remonter jusqu'aux premiers noyaux osseux tels qu'ils se montrent dans le fœtus."

The rule laid down by the French authorities above-cited fails in its application to the difficult question of the nature and number of bones in a skeleton, because they did not distinguish between those centres of ossification that have homological relations, and those that have only teleological ones; *i. e.* between the separate points of ossification of a human bone which typify vertebral elements, often permanently distinct bones in the lower animals; and the separate points which, without such signification, facilitate the progress of osteogeny and have for their obvious final cause the well-being of the growing animal. The young lamb or foal, for example, can stand on its four legs as soon as it is born; it uplifts its body from the ground and soon begins to run and bound along. The shock to the limbs themselves is broken and diminished at this tender age, by the divisions of the long bones, and by the interposition of the cushions of cartilage between the diaphyses and epiphyses. And the jar that might affect the pulpy and largely developed brain of the immature mammal, is further diffused and intercepted by the epiphysial articular extremities of the bodies of the vertebræ.

We thus readily discern a final purpose in the distinct centres of ossification of the vertebral bodies and the long bones of the limbs of mammals which would not apply to the condition of the crawling reptiles. The diminutive brain in these low and slow cold-blooded animals does not demand such protection against concussion; neither does the mode of locomotion in the quadruped reptiles render such concussion likely: their limbs sprawl outwards and push along the body which commonly sweeps the ground; therefore we find no epiphyses at the ends of a distinct shaft in the long bones of saurians and tortoises. But when the reptile moves by leaps, then the principle of ossifying the long bone by distinct centres again prevails, and the extremities of the humeri and femora long remain epiphyses in the frog.

A final purpose is no doubt, also, subserved in most of the separate centres of ossification which relate homologically to permanently distinct bones in the general vertebrate series; it has long been recognised in relation to facilitating birth in the human fœtus; but some facts will occur to the osteogenist, of which the teleological explanation is by no means obvious.

One sees not, for example, why the process of the scapula which gives attachment to the pectoralis minor, the coraco-brachialis, and the short head of the biceps should not be developed by continuous ossification from the body of the blade-bone, like that which forms the spinous process of the same bone. It is a well-known fact, however, that not only in man, but in all mammals, the coracoid process is ossified from a separate centre. In the monotremes it is not only autogenous, but is as large a bone as in birds and reptiles, in which it continues a distinct bone throughout life. Here, then, we have the homological, without a teleological explanation of the separate centre for the coracoid process in the ossification of the human blade-bone.

This distinction in the nature and relations of such centres is indispensable in the right application of the facts of osteogeny to the determination of the number of essentially distinct bones in any given skeleton.

All those bones which consist of a coalescence of parts answering to distinct elements of the typical vertebra are 'homologically compound.'

All those bones which represent single vertebral elements are 'teleologically compound,' when developed from more than one centre, whether such centres subsequently coalesce, or remain distinct, or even become the subject of individual adaptive modifications, with special joints, muscles, &c. for particular offices.

In the human skeleton, the clavicles, the (thoracic vertebral) ribs, are instances of simple and truly individual bones. The occiput, sphenoid, ethmoid, temporal, superior maxilla, mandible, hyoid, scapula, the so-called true vertebræ, the sacrum and coccyx, the sternum, and ossa innominata are 'homologically' compound bones.

The two parietals are essentially like the frontal and vomer, one 'teleologically' compound bone: so, likewise, are the two nasals. And, if the view of the homology of the jointed filamentary skeleton of the rudimental ventral fin of the lepidosiren with the simple diverging appendages of the costal arches of the abdominal vertebræ be correct, then is not merely the mammalian femur a teleologically compound bone, but the whole skeleton of the hind-limb from the femur to the distal phalanges inclusive must be regarded as representing the essentially single vertebral element, here called 'diverging appendage,' subdivided according to the law of vegetative repetition of centres; which law is progressively overruled and masked by the supervention of the higher law of special modification and adaptation of such vegetative subdivisions to the exigences and habits and sphere of life of the species.

In many animals all the parts of the skeleton of the limbs, and in all animals some of the parts, are simple bones, in the sense of being developed from a single centre; but in none can they claim that essentially individual character which the clavicles and osseous parts of the ribs are entitled to, as being primary vertebral elements.

To trace the mode and kind and extent of modification of the same elementary parts of the typical segment throughout a large natural series of highly organized animals, like the vertebrata; and to be thus led to appreciate how, without complete departure from the fundamental type, the species are adapted to their different offices in creation, brings us, as it were, into the secret counsels that have directed the organizing forces*, and is one of the legitimate courses of inquiry by which we may be permitted to gain an insight into the law which has governed the successive introduction of specific forms of living beings into this planet.

Vertebræ of the Skull.—Since it has been found that the bones of the trunk maintain through every kind and degree of adaptive modification, whether as 'thorax,' 'carapace' or 'sacrum,' an arrangement into segments in the constitution and relative position of the parts of which the vertebral type has been universally recognised—let us next examine, without bias, and, if possible, without reference to or recollection of previous attempts, in the first instance, whether such type be traceable through the remaining anterior part of the axis of the endo-skeleton, which, like the thorax and pelvis, has received, on account of its degree of coalescence and other modifications, the special collective term of 'skull;'—or, whether nature has, in this part of the endo-skeleton, so far departed from the pattern on which all the rest is constructed, that we cannot, without manifest violence to her arrangements, demonstrate the segmental composition; or refer, without admitting modifications distinct in kind as well as degree from those that mark the vertebral character in the trunk, the constitution of such segments to the vertebral type.

Taking the conical skull of an ordinary osseous fish—that of the cod (*Morrhua vulgaris*) for example,—if we detach the bones which form its hinder extremity, or base, and which immediately precede and join the atlas, from those next in advance, we have the circle, or the base bone (1) and arch (2, 3, 4), represented in figure 1, and we also bring away, articulated therewith, an inferior or inverted arch with its appendages, represented in profile outline in fig. 5, 50–57: the arrow indicating the course of convergence, and its head the point of union, of the two flanks or crura, forming the closing point or crown of such inverted arch.

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* "— præsens esse cum artifex operatur et opus suum promovet."—Bacon.

We have thus removed a segment of the skull, and with as little or even less violence or disturbance to the other bones, than must have been used in detaching a similar segment from the thorax or pelvis of a land-animal. If we compare this cranial segment with the typical vertebra fig. 14, we recognise in the single median bone (1, fig. 1) the *centrum*, by its relative position and its articular surface for the atlas, which retains, moreover, the concave form characteristic of the vertebræ in the piscine class: in the pair of bones (2, 2), which articulate with the upper surface of the centrum, protect the sides of the epencephalon, and are perforated by the 'nervi vagi,' we have the *neurapophyses*: in the single symmetrical bone (3) which completes the arch, and terminates in a crest for the attachment of the uppermost or dorsal portions of the vertebral muscles continued from the trunk, we have the *neural spine*: and in the pair of bones (4, 4), wedged between this spine and the neurapophyses, which give attachment to the inferior arch of the segment (fig. 5, H i), and terminate in a free crest or spine for the attachment of the upper and lateral portions of the vertebral muscles, we have the *parapophyses*; for whose elevated position we have been prepared by their gradual ascent in the anterior vertebræ of the trunk. The rest of this natural segment has undergone the same kind of modification as the thoracic vertebræ present in higher animals (fig. 15), and which consists in the great expansion of the hæmal arch, the removal of the *hæmapophyses* (fig. 5, 52) from the centrum (*ib.* 1), and the interposition of elongated and deflected *pleurapophyses* (50, 51): finally, the great inverted arch, so formed, encompasses, supports and protects the heart, or centre of the hæmal axis. The elements of this arch are open to two interpretations according to the type of figure 15: either 50 may be *pl*, 51, *h* and 52 *h s*; or 50 and 51 may be a divided (teleologically compound) pleurapophysis, and 52 an unusually developed hæmapophysis: and this latter conclusion is more agreeable with the character of the vertebral segments of the trunk in fishes, in which the hæmal spines are absent, the hæmapophyses, when ossified, long and sometimes joined together at their lower ends, as *e. g.* in the first trunk-vertebra of *Argyreiosus vomer*, and the pleurapophyses sometimes, as *e. g.* in the sturgeon, composed of two or more pieces, set end to end. The condition of the pleurapophysis of the pelvic arch in the menopome (fig. 28, 62, *pl*), which sustains a radiated appendage (*ib.* A) of the hæmal arch of the occipital vertebra, indicates the true character of the pleurapophysis: and the modifications of this arch in the higher classes will be found to establish the accuracy of the general homology of the bone 52, with the hæmapophysial element, since the lower extremities of 52 are actually drawn apart and articulated to a hæmal spine, which completes the arch below in reptiles and birds (fig. 22, H *s*).

Even should there be error in assuming the subdivision of the pleurapophyses and the absence of the hæmal spine, in the particular determination of the constituent elements of the arch in question, yet the alternative is still within the recognised limits of the vertebral modifications of the trunk; and the want of unquestionable proof of the precise elements forms no valid objection to its general homology as a hæmal vertebral arch, expanded and modified after one or other of the types of those which, in the thorax of the air-breathing vertebrates, encompass and protect the more backwardly placed centres of the vascular system (heart and lungs); according to which types, for example, it may be either closed below by the meeting of the sternal ribs (hæmapophyses) or by the intervention of a single or divided sternal bone (hæmal spine). And, further, since in fishes, as the lowest class of vertebrata, the vegetative character of repetition of forms, proportions and composition in the successive segments of the skeleton prevails in a greater degree than in any of the higher classes, so we may conclude that this hæmal arch presents, by its articulation with the epencephalic neural arch, its normal position; and that the whole occipital vertebra here manifests its veritable and typical character.

As the hæmal arches in the trunk of fishes commonly support diverging appendages, which project freely outwards and backwards, but are hidden and buried in the muscular masses to which they give attachment, so the occipital arch, also, commonly supports its diverging appendages. They are absent in *Gymnothorax* and some other *Murænidæ*. The appendage is present in the form of a single multiarticulate filament in the eel-like protopterus* and lepidosiren†; it is modified by that mode of vegetative repetition which results in adding to the number of similar filaments directly articulated to the supporting arch; and is further complicated by the expansion or confluence of the proximal joints in different degrees as they recede from the supporting arch, so as to constitute definable segments of the appendage‡.

Such is the condition of the part in most osseous fishes, and such is shown in the diagram of the base of the appendage in figure 5; where the proximal segment consists of two broad and flat bones (*54* and *55*), the next segment of five narrower and shorter but thicker bones (*56*), and the last segment of more numerous bones of the primitive filamentary form and multiarticulate structure, which bifurcate and radiate as they recede from the centre of attachment.

We may connect the tendency to extreme and variable development in the peripheral parts of a vertebral segment, with the freedom which is the necessary consequence of their position: they are attached by one end only, they have not, therefore, that physical restraint to growth which may arise out of the fettering by both extremities, which characterizes the more central vertebral elements entering into the composition of the neural and hæmal arches. Even in these we find the disposition to luxuriant growth or vegetative subdivision greatest in the peripheral elements, viz. the neural and hæmal spines: much more, therefore, might it be expected in the less constant, diverging, and commonly freely projecting appendages of the vertebral arches. Although here the polarizing forces which tend to shoot out particle upon particle after the pattern of dendritic corals, plants or crystals, are so controlled by the antagonizing principle of adaptation, that the radiating growth is always checked at that stage and guided to that form which is suited to the wants and required by the mode of life of the species.

Since, however, we are able to retain firmly and with certitude our recognition of the special homology of the diverging appendage of the occipital hæmal arch, through all its modifications, from the single ray of the lepidosiren to the hundred-fold repetition of the same elements with superadded dichotomous bifurcations sustaining the enormous pectoral fins of the broad and flat plagiostomous fishes thence called 'rays' *par excellence*, so we can retrace, with equal certitude, the serial homology of this appendage, when it is so plainly manifested by its simple form as well as connections in the lepidosiren, the amphiuma or the apteryx, with the scarcely more simple or less-developed appendage of the thoracic abdominal hæmal arches (ribs) of birds and fishes (figs. 15 and 17, *a*, *a*); and thus we are led to determine its general homology, under its manifold forms of fin, fore-limb, wing, or arm, as the diverging appendage of the hæmal arch of the occipital vertebra.

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* Linnean Transactions, vol. xviii. pl. 23, fig. 4, *55*.

† Bischoff, *Lepidosiren paradoxa*, 4to, pl. 2, fig. 4, *e*.

‡ Hunterian Lectures on Vertebrata, figs. 27, 40, 41, 42, 43, *55*.

The natural and typical vertebral segment above-defined cannot be detached, in every fish, by the mere disjunction of sutures: in the lepidosiren, *e. g.* the ossified part of the centrum has coalesced with that of the next segment in advance and would require to be divided by the saw: the same coalescence occurs in the human skull, and has led to the definition of the cranial bone, called 'os spheno-occipitale*.' In osseous fishes, either by connation of 5 with 9, fig. 5, or by excessive development of bone in the notochordal capsule extending forwards from the centrum 5, and producing 9, there results the long bone (5, 9) continuing the series of vertebral centrums forwards, and corresponding in position with two segments or arches above. On the hypothesis that it represents the central elements of both those arches, it must be divided artificially, in order to separate that segment of the cranium which next succeeds the occipital one. And, further, either by a similar coalescence of the proximal elements of two hæmal arches, or by the undue extension of such element of one of the arches, interposing itself between the next arch and the rest of the vertebra to which that arch belongs, it happens, that unless the proximal element or elements in question be artificially divided, as at 28*a*, 28*a*, fig. 5, two hæmal arches (H II and H III) would be brought away, with the neural arch detached by the separation of sutures and the division of the bone 5, 9. If neither that bone, nor 28*a* were divided, but were, with the bones in superior connection with them, separated from the bones anteriorly articulated to them by suture, then we should have the group of bones, included by the curved lines marked N II, N III, H II, H III in fig. 5. Two vertebral segments are plainly indicated in this group by the distinct hæmal arches and their appendages, H II and H III; but three pairs of bones, 16, 6 and 10, fig. 5, appear to be in neurapophysial relation with the single and symmetrical median bone 5, 9. If, however, what has been urged in the chapter on 'Special Homology' (pp. 188-196) respecting the petrosal character of 16 be a true interpretation of that bone, then we must eliminate it from our present inquiry, inasmuch as being a partial ossification of a sense-capsule (and nature herself removes them, as such, in most fishes), it appertains to a category of bones (splanchno-skeleton), forming no part of the proper neuro- or endo-skeleton, in which alone we seek for evidence of a segmental disposition of parts corresponding with the segments of the nervous system.

The bony petrosals (16) being removed, let us, then, with the view of examining the composition of the segment of the skull with which the occipital vertebra was articulated, saw across the bones 5, 9 and 28*a*, and separate the bones 6, 7, 8 from their sutural connections with those in front of them. In thus obtaining the segment in question, the opponents to the vertebral theory of the skull are entitled to assert that violence is done to nature by the sections of the single bones above-cited; the validity of which as an objection to that theory will be afterwards inquired into.

It is not, however, absolutely necessary to divide the basal bone 5, 9: in many osseous fishes a symmetrical bone (fig. 5, 9′) supports the parial bones 10, and stands in the relation of a centrum to them; the neural arch or circle of that segment would not, therefore, be broken by the removal with the posterior segment of the whole of the bone 5, 9. If the corresponding

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* See Table I., Soemmerring.

development from the under part of the centrum of the second cervical vertebra of the siluroid fish (p. 260) were removed, with that segment, from the atlas, the atlantal neural arch would still be completed by the rudimental body, beneath which the ossification from the succeeding vertebræ had extended itself.

Whether, however, we divide or not the bone 5, 5, those which rest upon its posterior or basisphenoidal part present, after the removal of the petrosals, when viewed from behind, and slightly disarticulated from each other, the arrangement exhibited in fig. 2. The bones 6, 6 support and defend the lobe of the third ventricle or the mesencephalic segment of the brain; they give exit to the trigeminal nerves (*tr*), and thus, as well as by their connections with the other bones of the arch, repeat the *neurapophysial* characters of the bones 2, 2 in the occipital segment. The bones 8, 8, by their more external position, by affording an articular surface to the hæmal arch (28*a*, H II), and their development of a strong transversely and backwardly produced process for muscular attachments, obviously repeat the *parapophysial* characters of the bones 4, 4 in the occipital vertebra.

The arch is not completed above in the cod-fish; the bones 7, 7 being separated at the mesial line by the interposition of the produced spine of the occipital vertebra 3, which joins with 11. In some other fishes, however, *e. g.* carp and pike, the bones 7, 7 do come in contact and join each other by a 'sagittal' suture, thus completing the neural arch. It will afterwards be seen, by tracing the homologues of these bones in other animals and their homotypes in other segments, what value may be assigned to the objection to their general homology as the crown or hæmal spine of the mesencephalic neural arch, founded upon the median division and occasional divarication of the two halves of no. 7 in osseous fishes. I may so far anticipate the discussion as to remark that, even in the present group of vertebrates, the spine of the occipital vertebra (3) is divided by a median suture in the lepidosteus; so that the condition of the epencephalic arch in that fish is precisely that of the mesencephalic arch in the carp, and essentially the same as that in fig. 2, and in most other osseous fishes.

The remainder of the second or parietal segment of the skull, H II, repeats the expanded modification of the hæmal arch of the occipital vertebra, and even approaches nearer to the character of the thoracic vertebræ of the higher animals, by the development of single symmetrical bones at the crown of the inverted arch. But the principle of vegetative repetition is still more manifested in this arch than in the occipital one. If we regard the posterior half of the epitympanic, 28*a*, as the proximal piece of the parieto-hæmal arch, which has coalesced with the corresponding piece of the fronto-hæmal arch, then the *pleurapophysis* of the parieto-hæmal arch will consist, in bony fishes, of two pieces, 28*a* and 38, like the pleurapophysis of the occipito-hæmal arch, 50 and 51. The bones, 38 and 40, represent the *hæmapophysis* of the parieto-hæmal arch. The two pairs of small bones (41) with the single median anterior (42) and posterior (43) appendages, represent a still more subdivided spine or keybone of this inverted arch.

Beneath this mask of multiplication of bony centres, the broad characters of the inverted arch suspended to the parapophyses of the parietal vertebra, as the hæmal complement of that natural segment of the skull, stand boldly out: it encompasses, sustains and protects the branchial organs—the analogues of lungs—the next great development of the vascular system anterior to the heart; and the subdivision of the piers of this expanded arch relates to the necessity for a combination of strength, with flexibility and elasticity, in the execution of the movements producing the respiratory currents.

The correspondence with the scapular, or occipito-hæmal arch, is further carried out by the presence of *appendages* (44) which freely diverge from it, but the development of these appendages has not been observed to extend beyond that second phase, marked by vegetative multiplication of the simple ray, directly attached to the arch itself. The lepidosiren offers the simplest condition of such 'diverging appendage' in the single slender bony piece connected with the element 40*. Cuvier and other ichthyologists cite a series of stages of this kind of development of the hyoidean appendage from a similar simple beginning up to a 30-fold repetition of the single ray (*Elops*); and the 'branchiostegal' rays have been found in much greater numbers in certain fossil fishes. Like the 'pectoral' rays, they support a duplicature of membrane, which plays freely backwards and forwards, reacting upon the ambient medium, and forming, in short, a cephalic fin, but with its powers so restricted and adjusted, as to propel the water through the branchial chambers of the fish, instead of driving the fish through the water; in which latter action, indeed, the occipital appendages (pectoral fins)in most osseous fishes can and do perform but a very small share.

If we next proceed to compare the frontal segment, N III and H III, dismembered as above described from the parietal vertebra, and, by the separation of the sutures, from the bones terminating the skull anteriorly, we shall find a neural arch (fig. 3) closely repeating the characters of that of the occipital vertebra. The *centrum* is sometimes represented simply by the forward extension of ossification of the basisphenoid (11), which I regard as the homotype of the ossification of the capsule of the notochord beneath the centrums of the anterior trunk-vertebræ in the silurus; sometimes, also, of a distinct superincumbent symmetrical ossicle (9', fig. 5), answering to the rudimental (central part of the) body of the atlas supported by the inferior bony plate, in the silurus. This more complex condition of the centrum of the frontal vertebra is well-seen in the sword-fish. The bones 10, 10, which directly rest upon 9', when it exists, which defend the sides of the prosencephalon, and which are either grooved by the optic nerves, or have those nerves perforating the fibro-cartilaginous membrane close to the margin of the bone (10) from which it is continued, are obviously the *neurapophyses*. They are, however, small; inasmuch as the segment of the brain to which they relate is of inferior size in bony fishes: and they are still smaller in comparison with the spine (11) which is enormously expanded, in relation to its accessory functions as the chief contributor to and protector of the orbits. The bones 12, wedged between the neurapophyses and spine, affording an articular surface to the proximal piece of the hæmal arch, and developing a transverse process for muscular attachments, are the *parapophyses*. The bones (17) have as little essential connection with the typical neural arch above demonstrated, as the bones 16, 16'' had with the corresponding arch of the parietal vertebra: and their more peculiar form in relation to the ball which they protect, and their variable histological condition in the vertebrate series, have not only prevented their ever being mistaken for parts of cranial vertebræ, but have led to the opposite extreme of excluding them altogether from the bones of the skull, with which they are as much entitled to rank as the petrosal (16) or the turbinal (19); but always in the category of sense-capsules or 'splanchno-skeletal' pieces.

In regard to the inferior arch of the frontal segment, the subdivision of its constituent elements, in subserviency to its special functions, is carried to as great an extent as in that of the parietal segment. I regard the four overlapping and closely-connected pieces from the upper joint (28) to the lower

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* Hunterian Lectures on Vertebrata, p. 79, fig. 27, 40.

joint (28*d*) inclusive, as the *pleurapophysis*: it is not so obvious whether the bones 29–32 form a subdivided *hæmapophysis*, or whether the terminal bone (32), forming by symphysis with its fellow the crown of the inverted arch, may not be the moiety of a mesially divided *hæmal spine*. But the general character of the inverted arch (H III), as the hæmal complement of the frontal vertebra is unmistakeable, and its serial homology with the succeeding arches (H II and H I) is fully illustrated in fishes by its supporting *diverging appendages* (34–37). These, in the series of fishes, manifest, in as many permanent arrests, the chief phases of development that the corresponding appendages of the occipito-hæmal arch have been described to pass through. The diverging appendage of the fronto-hæmal arch is a single and simple bony style in the lepidosiren; it consists of three or four simple rays in the monk-fish and some other plagiostomes; it has one ray expanded into a broad proximal piece in the conger, which sustains a distal segment of the appendage, one member of which, the 'subopercular,' still retains the long and slender, ray-like form, which is, also, clearly traceable in the broader but long and curved 'opercular'; in the cod, as in most osseous fishes, the parts of the second segment of the appendage (35, 36, 37, fig. 5) are metamorphosed, like the proximal one (34), into broad and flat bones. The fin-like fold of integument, sustained and moved by means of this diverging appendage and its muscles, reacts upon the surrounding water; but, like the hyoid-fins, with which the tympanic or opercular fins ara closely connected, they are chiefly subservient to the creation of the respiratory currents and their direction through the gill-chambers. The weight of these appendages, and the constant movements in connection with respiration, as well as those which the hæmapophysial portions of the arch, modified in subserviency to nutrition have to perform, as jaws, explain the necessity of the subdivision of the supporting pedicle into overlapping pieces allowing of a certain elastic yielding with recoil, and thus diminishing the liability to fracture without affecting, except by increasing, the strength of the arch. The trochlear joint between the two elements of this arch (at 28*d* and 29) with its cartilage and synovial sac, repeats the complex structure of the articulation between the vertebral and sternal portions of the ribs in birds. To the fore-part of the lower piece (28*d*) of the pleurapophysis is usually articulated a bone (24) connecting it with another bone (20) in advance: the ground for regarding 24 as appertaining to the arch (20, 21 and 22, H IV) will be explained in the description of that arch.

There remains, then, in the fish's skull, to be considered, the group of bones (N IV, H IV, fig. 5) forming its anterior extremity; and we have to inquire, whether there can be traced in this easily separable group such a concordance in its formation with the arrangement of the constituents of the foregoing segments as will justify its being regarded as a natural segment of the skull, and as still illustrating the type on which all the other segments of the endoskeleton have been constructed. Fig. 4 gives the same view of the bones of this group in vertebral relation with the rhinencephala as the views in figs. 1, 2 and 3 do of the bones having a similar relation to the three larger segments of the brain: we perceive the single and symmetrical bone (13) forming the basis of the arch, and sustaining the bones 14, 14, which more immediately support the olfactory ganglions and transmit their nerves, either by grooves or foramina, to the olfactory capsules: the key of the arch is formed by the single and symmetrical bone 15, which is articulated to and chiefly sustained by the bones 14, 14: but 15 is expanded and deflected anteriorly so as to rest directly upon 13 and completely obliterate the neural canal; the hæmal canal being in like manner closed by the approximation of the hæmal spine (22) to the nasal centrum (13), and by the upward development of the processes of 22 which join the neural spine (15). Much modification was to be expected in the segment which terminates the skeleton anteriorly; and yet the typical characters of the neural arch are more completely preserved here than at the opposite end of the vertebral column. If the bones 4, 8, 12, which I recognise as 'parapophyses' in the cranial segments I, II, III, must be viewed as superadded intercalations for the special and characteristic expansion of the neural arches of those segments—normal elements, indeed, of the typical vertebra, but with modified connections for cranial functions—then the disappearance of their homotypes in the nasal segment restores its neural arch (fig. 4) to the more common condition, and we recognise in 13 the *centrum*, in 14, 14, the *neurapophyses*, and in 15 the *neural spine* of the nasal vertebra.

But the segment to be complete should exhibit a second arch, inverted; and we find such arch closed or completed by the symphysis of the bones 22, fig. *5*, and suspended to the sides of the centrum 13 and to the neurapophyses 14, 14, by the bones 20, as the piers or crura of the arch; these bones being connected to the key-bones 22, by the intermediate bones 21. Now, the modifications which these elements of the inverted or hæmal arch of the nasal vertebra have undergone, are, also, much less than might have been anticipated from the extent to which the segments are modified at the opposite extreme of the endoskeleton. All the normal elements of the hæmal arch, for example, are retained: 20 is the *pleurapophysis*, 21 the *hæmapophysis*, and 22 the *hæmal spine*, in most fishes divided at the middle line, but sometimes confluent with its fellow *e. g. Diodon*. The essential (pleurapophysial) part of 20 extends in many fishes (*e. g.* percoids) like a short straight rib from its articulation with 13 and 14 to the condyle at its opposite end to which the hæmapophysis 20 is articulated; but it usually, also, developes a process from its hinder margin downwards and backwards, which gives attachment to the diverging appendage of the arch H IV. The development of the other bones of the arch, 21 and 22, outwards, downwards and backwards, is still more marked in relation to the protractile and retractile movements of the arch in most osseous fishes; and some anatomists, influenced by the form and proportions rather than the connections of those bones, have described them as independent parallel arches: but, as such, they must be regarded as being suspended by their apices or key-stones to the axis of the skull, and as having their haunches hanging freely downwards and outwards—a position the reverse of that of the foregoing inferior arches of the skull and of every typical hæmal arch. The reduction of that divergent development, characteristic of the bones 21 and 22 in fishes, is effected in a great degree within the limits of the piscine class: already we find one of the spurious arches abrogated in the salmonoid fishes by the shortening of 22, and its more direct continuation from 21, which now forms the larger part of the upper border of the mouth and supports teeth: the confluent maxillaries and premaxillaries send down only a single divergent process from their point of suspension to the palatine condyle in the plectognathic fishes; and the consolidation of all the elements of the palato-maxillary arch into its normal unity is effected in the lepidosiren*. The palatines (20) always form the true bases or suspensory piers of the inverted hæmal arch at their points of attachment to the prefrontals (14); the premaxillaries, 22, constitute the true apex or crown at their symphysis or point of confluence, H IV; the approximation of which to the anterior end of the axis of the skull is rendered possible, in fishes, by the absence of any air-passage or nasal canal. The diverging appendage, sometimes single and anchylosed to the arch (lepidosiren); sometimes single and detached like a long, narrow bone (some murænoids); more commonly consists of two bones (23, 24), which extend outwards, downwards, and backwards from the pleurapophysis (20); but the more constant and better ossified bone of the two, no. 24, articulates posteriorly with the succeeding pleurapophysis (20) and combines its movements with those of its own arch, just as the diverging appendages of one thoracic hæmal arch in the bird associate the movements of that arch with those of the next in succession (as in fig. 15, *pl*, *a*, *pl*). The hæmapophyses here, as at the opposite end of the body, begin so far to dissociate themselves from the pleurapophyses as to articulate also directly with the centrum (13) as well as with the pleurapophyses. I regard this as a very interesting approximation to that condition of the typical vertebra which is illustrated by the diagram (fig. 14), and which is seen in nature in the caudal vertebræ of the crocodiles, enaliosaurs and menopome (fig. 28, H).

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* Hunterian Lectures, Vertebrata, p. 81, fig. 23.

From the foregoing analysis it appears, then, that in osseous fishes the endoskeletal bones of the head are arranged, like those of the trunk, in segments; that these are four in number, and that they closely conform to the character of the typical vertebra.

Thus we have four centrums and neural arches: viz.

N I. Epencephalic arch (figs. 1 and 5, 1, 2, 3, 4);
N II. Mesencephalic arch (figs. 2 and 5, 5, 6, 7, 8);
N III. Prosencephalic arch (figs. 3 and 5, 9, 10, 11, 12);
N IV. Rhinencephalic arch (figs. 4 and 5, 13, 14, 15).

As a collective name for the sum of these immoveably articulated arches would be as convenient as the anatomist finds the names 'sacrum' and 'carapace,' applied to similarly consolidated portions of vertebral segments in the pelvic and abdominal regions of certain air-breathing vertebrates, that of 'cranium' may well be retained for the neural arches of the skull: but it should be understood to signify, in all animals, the bones 1 to 15 inclusive; whereas it has, hitherto, been applied variably in different species; sometimes including sense-capsules and facial bones, intercalated to expand the walls of the cavity for a large brain; and more frequently excluding true cranial bones, those of the rhinencephalic arch, for example, which encompass as essential a part of the encephalic chamber, as the sacral vertebræ do of the neural canal at the opposite end of the vertebral axis; although in both instances the extremities of the neural axis may have been withdrawn, in the course of its concentrative change and movement, from their original seat.

The hæmal arches indicated by the arrows in fig. 5, the heads marking the point of junction or crown, are,—

H I. Scapular arch (50–52);
H II. Hyoidean arch (38–43);
H III. Mandibular arch (28–32);
H IV. Maxillary arch (20–22).

The diverging appendages of the hæmal arches are,—

1. The Pectoral (54–57);
2. The Branchiostegal (44);
3. The Opercular (34–37);
4. The Pterygoid (23–24).

The bones or parts of the splanchno-skeleton which are intercalated with or attached to the arches of the true vertebral segments, are,—

The Petrosal (16) or ear-capsule, with the otolites, 16″;
The Sclerotal (17) or eye-capsule;
The Turbinal (18) or nose-capsule;
The Branchial arches;

The Teeth.

The bones of the dermo-skeleton are,—

- The Supratemporals;
- The Supraorbitals;
- The Suborbitals;
- The Labials.

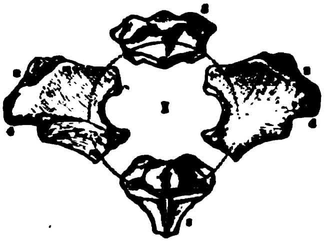
Such appears to be the natural classification of the parts which constitute the complex skull of osseous fishes.

As the object of the present work relates chiefly to the endoskeleton, I have only added the osseous parts of the sense-capsules to the cranial vertebræ in fig. 5; omitting the branchial arches and dermal bones: the hæmal arches and their appendages are given in diagrammatic outline.

Reptiles.—In proceeding with the inquiry into the natural arrangement of the skull-bones, I have selected from the *Reptilia* the crocodile, as a typical example of that class, and one most likely to facilitate the inquiry on account of the characteristic persistence of the primitive cranial sutures.

Pursuing the same mode of investigation as in the case of the fish, let us disarticulate the hindmost segment of the skull and so detach the four bones, represented in fig. 18. The dotted circle indicates the points at which these bones are joined together, in order to encompass the epencephalon, or hindmost segment of the brain. No. 1 is the *centrum*; 2, 2 are the *neurapophyses* with the coalesced *parapophyses* (4, 4); and 3 is the *neural spine*. This element differs but little in size and shape from the similarly detached and depressed neural spine of the atlas of the crocodile. The single convex condyle at the back part of no. 1 makes that centrum resemble the posteriorly convex bodies of the trunk-vertebræ in as striking a manner as the repetition of the articular concavity in the basioccipital of the cod (fig. 1, 1) marks its serial homology with the succeeding vertebral centrums of the same animal. In the descending process from the under part of the occipital centrum of the crocodile (fig. 18, 1), we see a second character of the cervical centrums in that reptile repeated, viz. their inferior exogenous spine. The neurapophyses (2, 2), like those of the atlas, meet above the neural canal: they give exit to the vagal and hypoglossal nerves, and protect the sides of the medulla oblongata and cerebellum. The neural spine (3) protects the upper surface of the cerebellum: it is also traversed by tympanic cells, and assists, with the bones 2, 2, in the formation of the chamber for the internal ear. The special homology of the outstanding processes (4, 4) in the crocodile and serpent (fig. 10), with the similarly situated but distinct 'paroccipital' bones in the cod, is confirmed by their resuming their independency in the hinder segment of the skull of the chelonian reptiles; and the occipital neural arch of the crocodile is reduced by their confluence with the neurapophyses to the condition of those of the trunk-vertebræ, as composed, viz. of four instead of six elements.

Fig. 18.



Disarticulated epencephalic arch, viewed from behind: Crocodile.

The epencephalic arch offers the same simple condition not only in the ophidians but in most saurians: the chameleons however retain, like the chelonians, the ichthyic independence of the parapophyses (*4*, *4*). In batrachians the epencephalic arch is reduced to the two important elements, the neurapophyses; which meet and join each other below as well as above the foramen magnum, and develope the exogenous zygapophyses, or two occipital condyles, for articulation with the corresponding processes of the neural arch of the atlas. The basioccipital, if it exists in batrachians, is rudimental and confluent with the basisphenoid, and the supraoccipital is in like manner recognisable only as the posterior border of the backwardly produced parietal. The parapophyses are short exogenous processes of the neurapophyses of this much simplified epencephalic arch in all batrachian reptiles.

The chief modification that distinguishes the above-described segment of the crocodile's skull from its homologue in the fish, is the absence of an attached inverted or hæmal arch. We recognise, indeed, the special homologues of the piscine constituents of that arch in *50*, *51* and *52*, fig. 22. The upper suprascapular piece (*50*) is however free, disconnected from any segment, and retains, in connection with the loss of its proximal or cranial articulations, its cartilaginous state: the scapula (*51*) is ossified, as is likewise the coracoid (*52*), the lower end of which is separated from its fellow by the interposition of a median, symmetrical, partially ossified piece called 'episternum' (*hs*). The power of recognising the special homologies of *50*, *51*, and *52* in the crocodile, with the similarly numbered constituents of the arch H I in fishes (fig. 5), though masked not only by modifications of form and proportion but even of very substance, as in the case of *50*, depends upon the circumstance of these bones constituting the same essential element of the archetypal skeleton: for although in the present instance there is superadded to the adaptive modifications above-cited the rarer one of altered connections, Cuvier does not hesitate to give the same names (suprascapulaire) to *50* and (scapulaire) to *51*, in both fish and crocodile: but he did not perceive or admit that the narrower relations of special homology were a result of, and necessarily included in, the wider law of general homology. According to the view of this law here taken, we discern in *50* and *51*, fig. 22, a teleologically compound *pleurapophysis*, in *52* a *hæmapophysis*, and in *hs* the *hæmal spine*, completing the hæmal arch.

The general relations of the scapulo-coracoid arch to a hæmal or costal one have been long recognised, but the vertebral segment to which it appertains seems not hitherto to have been suspected, and has certainly not been satisfactorily determined. Oken, who had observed the free cervical ribs in a specimen of the *Lacerta apoda*, Pallas (*Pseudopus*), deemed them representatives of the scapula, and this bone to be, in other animals, the coalesced homologues of the cervical pleurapophyses*. In no animal are the conditions for testing this question so favourable and obvious as in the crocodile: not only do cervical ribs coexist with the scapulo-coracoid arch, but they are of unusual length and are developed from the atlas as well as from each succeeding cervical vertebra: we can also trace them beyond the thorax to the sacrum, and throughout a great part of the caudal region, as the sutures of the apparently long transverse processes of the coccygeal vertebræ demonstrate in the young animal; the lumbar pleurapophyses being manifested at the same period as cartilaginous appendages to the ends of the long diapophyses.

* "Auch die Scapula nicht *ein* Knochen, sondern wenigstens eine aus fünf Halsrippen zusammengeflossene Platte ist."—Programm, &c., 4to, 1807, p. 16. He reproduces the same idea of the general homology of the scapula in the 'Lehrbuch der Natur-philosophie,' 1843, p. 331, ¶ 2381. Carus also regards the scapulo-coracoid arch as the reunion of several (at least three) protovertebral arches of the trunk-segments. 'Urtheilen des Knochen und Schalen gerustes, fol. xxxiii.

The scapulo-coracoid arch, both elements of which retain the form of strong and thick vertebral and sternal ribs in the crocodile, is applied in the skeleton of that animal over the anterior thoracic hæmal arches. Viewed as a more robust hæmal arch, it is obviously out of place in reference to the rest of its vertebral segment. If we seek to determine that segment by the mode in which we restore to their centrums the less displaced neural arches in the sacrum of the bird (fig. 27, *n* 1–*n* 4), we proceed to examine the vertebræ before and behind the displaced arch with the view to discover the one which needs it in order to be made typically complete. Finding no centrum and neural arch without its pleurapophyses from the scapula to the pelvis, we give up our search in that direction; and in the opposite direction we find no vertebra without its ribs until we reach the occiput: there we have centrum and neural arch, with coalesced parapophyses—the elements answering to those included in the arch N 1, fig. 5—but without the arch H 1; which arch can only be supplied, without destroying the typical completeness of antecedent cranial segments, by a restoration of the bones *50–52*, to the place which they naturally occupy in the skeleton of the fish. And since anatomists are generally agreed to regard the bones *50–52* in the crocodile (fig. 22) as specially homologous with those so numbered in the fish (fig. 5), we must conclude that they are likewise homologous in a higher sense; that in fig. 5 the scapulo-coracoid arch is in its natural or typical place, whereas in the crocodile it has been displaced for a special purpose. Thus, agreeably with a general principle, we perceive that as the lower vertebrate animal illustrates the closer adhesion to the archetype by the natural articulation of the scapulo-coracoid arch to the occiput, so the higher vertebrate manifests the superior influence of the antagonising power of adaptive modification by the removal of that arch from its proper segment.

The scapula retains the more common cylindrical long and slender rib-like form of the pleurapophysis in the chelonian reptiles, where, from the greater length of the neck, it has retrograded further than in the crocodile from its proper centrum, and is placed not upon, but within, an anterior thoracic hæmal arch, the pleurapophysis of which has, on the other hand, been expanded like a scapula.

If the arguments founded upon the relations of the scapulo-coracoid arch to the segments of the skeleton in osseous fishes and crocodilians be admitted to sustain the conclusion here drawn from them, that arch must be held to form the hæmal complement of the occipital vertebra in all animals. Bojanus, in illustrating his vertebral theory of the skull by the osteology of the *Emys Europæa*, thus defines the

"Vertebra occipitalis, sive capitis prima.
"Basis occipitis, seu *corpus* hujus vertebræ,
"Pars lateralis occipitis, sive *arcus*,
"Crista occipitalis, *processus spinosi* loco,
"Cornu majus hyoidis, *costæ vertebræ* occipitalis comparandum *."

He adds a dotted outline of the hyoid arch to complete the *vertebra occipitalis*, in tab. xii. fig. 32, B. 1 of his beautiful Monograph.

Supposing the special homology of the middle cornua of the hyoid of the chelonian, so represented and compared to ribs by Bojanus, with the stylo-, epi- and cerato-hyals of the fish (fig. 5, *38*, *39*, *40*) to have been correct, which the metamorphoses of the hyoid and branchial arches in the batrachians disprove, the singular and highly interesting change of position as well as shape of the true ceratohyals, during the same metamorphosis, prepares us to expect a retrogradation of the hyoid arch in respect to its proper centrum, in the

* Anatome Testudinis Europææ, fol. 1819, p. 44.

skulls of the air-breathing vertebrates. In the young tadpole the thick cartilaginous hyoidean arch[*] is suspended, as in fishes, from the tympanic pedicle: the slender hyoidean arch of the mature frog is suspended from the petrosal capsule[†]. The mandibular arch has, also, receded; and the scapular arch which, at its first appearance, was in close connection with the occiput, further retrogrades in the progress of the metamorphosis to the place where we find it in the skeleton of the adult frog.

The argument, therefore, may be summed up as follows. The position of the neurapophyses in the dorsal vertebræ of chelonians and in the sacral vertebræ of dinosaurians and birds, shows that a change of relative position in respect of other elements of the same vertebra may be one of the teleological modifications to which even the most constant and important elements are subject. Instead of viewing such shifted arches as independent individual parts, we trace their relation to the stationary elements of the vertebral segments—the centrums. Thus, commencing, for example, with the anterior of the sacral vertebræ of the ostrich, A in fig. 27, we observe that, besides supporting its own neural arch, it bears a small portion of that of the next vertebra: the third neural arch (n_1) has encroached further upon the centrum of the vertebra in advance; and thus, in respect to the neural arch (n_2), if it were viewed with the centrums, c_2 and c_1, upon which it equally rests, apart from the rest of the sacrum, it would appear to appertain equally to either, and be referable to the one in preference to the other quite gratuitously. Nevertheless n_2 is proved, by the intermediate changes in antecedent neural arches, to belong actually, and in no merely imaginary or transcendental sense, to c_2 altogether, and not to the segment of which c_1 is the centrum; and in tracing the modifications of those sacral vertebræ which follow c_2, we find n_4 to have regained nearly the whole of its centrum, c_4, and the normal relations of the elements are quite restored in the succeeding vertebra.

Now let us suppose the habits of the species to have required a more extensive displacement of the arch (n_2) and its appendages: if its formal characters as a neural arch were still retained beneath the adaptive development superadded to the adaptive dislocation, and if the segments before and behind the centrum c_2 were found complete, and that centrum alone wanting its neural arch; would the mere degree of modification in respect of relative position nullify the conclusion that the shifted arch appertained to such incomplete segment, and forbid that restoration to the typical condition, which no anatomist, it is presumed, will dispute in the case of n_2, c_2, fig. 27? No anthropotomist hesitates in pronouncing the exact vertebra to which the sixth ribs belong in the human skeleton. But, separate that costal arch with the two bodies and neural arches of the vertebræ with which it articulates, and to which of them it belonged would be as questionable as in the instance of the displaced neural arch in the bird's sacrum. The head of each rib is applied half to the upper centrum, half to the lower one: the upper border of the neck of the rib articulates with the upper neural arch, the tubercle with the diapophysis of the lower neural arch. If a naturalist, not conversant with the definitions of human anatomy, were shown this detached part of the human skeleton and were pressed to determine the proper centrum and neural arch of the hypothetically displaced costal element, the attempt might seem to him gratuitous: and to the question, to which of such centrums the rib exclusively (as to the pre-existing pattern) belonged? he might reply, to neither. And such, doubtless, would be the matter-of-fact answer most congenial to the character of mind which would limit its views to the specialities of the ribs as parts independent of any ideal archetype, or be unable or unwilling to push the consideration of their connections beyond the purposes apparently subserved thereby. A second anatomist might see in the more constant articulation of the costal tubercle with the transverse process, a character which would incline the balance in favour of the vertebra to which the transverse process belonged. A third anatomist might extend his comparisons to other ribs and centrums, and finding the lower centrum obtaining by degrees a greater proportion of the head of the rib, until the first and last ribs respectively wholly articulated to the centrum answering to the lower one in the case of the hypothetically detached sixth pair, he would conclude that such pair of ribs belonged essentially to the lower and not to the upper supporting centrum, and he would count accordingly such lower centrum with its neural arch, as the sixth of those vertebræ which are characterized as supporting ribs. The anthropotomist, in fact, in so counting and defining the dorsal vertebræ and ribs, admits unconsciously perhaps, an important principle in general homology, which pursued to its legitimate consequences and further applied, demonstrates that the scapula is the modified rib of that centrum and neural arch which he calls the 'occipital bone,' and that the change of place which chiefly masks that relation (for a very elementary acquaintance with comparative anatomy shows how little mere form and proportion affect the homological characters of bones) differs only in extent and not in kind from the modification which makes a minor amount of comparative observation requisite in order to determine the relation of the shifted sixth rib to its proper centrum.

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[*] Cuvier, Ossem. Foss. v. pt. ii. pl. 24, fig. 23, *a*.

[†] *Ib*. fig. 27, *a*:—an intermediate stage is shown at fig. 25. Dugés and Reichert confirm and further illustrate this change of position of the hyoidean arch.

With reference, therefore, to the occipital vertebra of the crocodile, if the comparatively well-developed and permanently distinct ribs of all the cervical vertebræ prove the scapular arch to belong to none of those segments, and, if it be wanting to complete the occipital segment, which it actually does complete in fishes, then the same conclusion must apply to the same arch in other animals, and we must regard the occipital vertebra of the tortoise as completed below by its scapulo-coracoid arch, and, not as Bojanus supposed, by its hyoidean arch*.

With these views of the general homology of the scapulo-coracoid arch, the embryologist will observe with less surprise its constant appearance in the first instance close to the occiput, and its equally constant primitive vertical position; however far back it may be subsequently removed, or to whatever extent it may be rotated, in the same progress to maturity, out of its original parallel direction with the more normal pleurapophyses.

Returning to the study of the crocodile's skull in reference to the vertebrate archetype, if we proceed to dislocate the next segment in advance of the occipital, we bring away in connection with the long base-bone, 5 and 9, fig. 22, the bones connected by the double lines N II, N III, and by the

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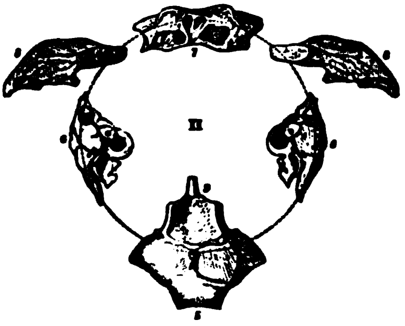
* Geoffroy St. Hilaire selected the opercular and subopercular bones to form the inverted arch of his seventh (occipital) cranial vertebra (Table III. and note 11), and took no account of the instructive natural connections and relative position of the hyoidean and scapular arches in fishes. With regard to the scapular arch, he alludes to its articulation with the skull in the lowest of the vertebrate classes as an 'amalgame inattendue' (Anatomie Philosophique, p. 481); and elsewhere describes it as a "disposition véritablement très singulière, et que le manque absolu de cou et une combinaison des pièces du sternum avec celles de la tête pouvoient seules rendre possible."—Annales du Muséum, ix. p. 361. A due appreciation of the law of vegetative uniformity or repetition, and of the ratio of its prevalence and power to the grade of organization of the species, might have enabled him to discern the true signification of the connection of the scapular arch in fishes.

curved arrows H'II and H III. The relations of the superior series of bones as neural arches to the optic lobes and cerebrum are even less doubtful than in many fishes, by reason of the much smaller degree of independent ossification of the proper capsule of the acoustic labyrinth. Taking, then, the bones forming the arch N II, we find them, viewed from behind, to present the general arrangement shown in fig. 19. The hinder (basisphenoidal) portion of the bone 5 and 9 forms the *centrum*, and immediately supports the floor of the mesencephalon, or lobe of the third ventricle, being excavated for the pituitary prolongation of that cavity: it also sends a process downwards, repeating, like the basioccipital, the inferior exogenous spine of the centrums of the cervical vertebræ. The bones 6, 6 protecting the sides of the mesencephalon, and notched for the transmission of the trigeminal nerve, manifest the *neurapophysial* characters of the segment. As accessory functions they contribute, like the corresponding bones in fishes, to the formation of the ear-chamber. They have, however, a little retrograded in position (see fig. 9), resting below, in part, upon the occipital centrum, and supporting more of the spine of that centrum (3) than of their own (7); which is, however, formed of a single bone, and in so far manifests more of the normal character of the element completing the neural arch, as its crown or key-bone, than does the homologous divided and often divaricated bone in fishes. This and other analogous facts show that although the lowest vertebrate class adheres most, as a whole, to the archetype, yet that it can be recognised clearly and unequivocally only by patient study of its modifications in all classes: for even the lowest have special exigencies arising out of their sphere of existence calling for modifications of the type which are not present in other and higher classes. We shall find, indeed, that the connation of the basi- and pre-sphenoids ceases in mammals, and that they only coalesce in that class, being primitively distinct; so that the second cranial centrum (5) may be removed with its neural arch, in the fœtal quadruped (fig. 24) or human subject (25), without doing violence to nature by the use of the saw. The bones 8, 8, fig. 19, wedged between 6 and 7, here, also, manifest more of their *parapophysial* character than in fishes, inasmuch as they are excluded from the inner walls of the cranium, whilst they retain and manifest broadly their characters as outstanding processes for muscular attachment. But, besides affording ligamentous attachment to the hyoid arch (38, 40), they articulate largely with the proximal element (28) of the mandibular arch, whose backward displacement, in comparison with its more normal position in the fish's skull (fig. 5), is as clearly illustrated in the metamorphosis of the anourous batrachia, as is that of the hyoidean or scapular arches.

Fig. 19.



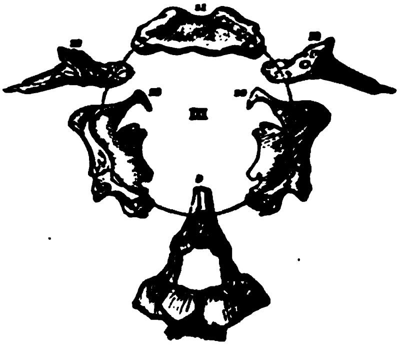
Disarticulated mesencephalic arch, viewed from behind: Crocodile.

Referring, then, to the side view of the cranial vertebræ of the crocodile (fig. 22), we see the hæmal arch of the second or parietal vertebra in the hyoid (38, 40, 41) retaining so much of its embryonic dimensions as is required by its restricted functions, and having no call for progressive growth in subserviency to a branchial respiration. It consists of a ligamentous stylohyal, its *pleurapophysis*, retaining the same primitive histological condition which obstructs the ordinary recognition of the same elements of the lumbar hæmal arches. The hæmopophyses and hæmal spine are, however, here as there, more advanced in respect of their tissue. The *hæmapophysis* is ossified like the so-called 'abdominal ribs,' and usually, like them, consists of two portions, having the special names of epihyal (39) and ceratohyal (40): the *hæmal spine* (41) retains its cartilaginous state like its homotypes in the abdomen: there they get the special name of 'linea alba' or abdominal sternum, here of 'basihyal.' With respect to formal modification, this element is chiefly remarkable in the crocodile for its broad expanse: it sustains the ascending valvular ridge at the base of the tongue, which, applying itself against the descending 'palatum molle,' constitutes an effectual barrier against the entry of water into the glottis from the mouth, whilst the crocodile is engaged in overcoming the struggles of a submerged and drowning prey.

There being no need of diverging appendages from the hyoidean arch in the crocodile, branchiostegal rays are not developed. The scapular arch is similarly simplified in *Anguis* and other serpentiform lizards; but, to those who recognise its true homology, its presence without a trace of its appendages, the fore-limbs, will create no more surprise, than the presence of the hyoidean arch without the branchiostegal fins or of the mandibular arch without the opercular fins.

On removing the neural arch of the parietal vertebra, with or without the section of the connate centrum (5), the bones completing, with the part (9), the corresponding arch of the frontal vertebra present the general arrangement shown in fig. 20.

Fig. 20.



Disarticulated prosencephalic arch, viewed from behind: Crocodile.

The compressed produced bone, 9, shown in natural connection with the bone 10 in fig. 9, notwithstanding its modified form, presents all the essential characters of the *centrum* of the arch: although it may have been developed exclusively from the capsule of the notochord, like the coalesced inferior parts of the cervical centrums in the silurus: there is no distinct ossicle answering to the central part of the centrum of the frontal vertebra, like $9'$, fig. 5, in certain bony fishes. On the other hand, we find the *neurapophysial* characters of the orbito-sphenoids (10, 10) more largely and typically manifested in the crocodile: they are smoothly excavated within by the sides of the prosencephalon: they dismiss the great special-sense nerves of the eye by the notch (fig. 9, op), and the motor nerves by the notch *s*: they show, however, the same tendency to change of position as the succeeding neurapophyses; for though they support a greater proportion of their proper spine (11), they also support part of the succeeding spine (7), and rest below in part upon the parietal centrum (5). The *neural spine* of the frontal vertebra (11) retains its normal character as a single symmetrical bone, like the parietal spine, which it partly overlaps. It is much developed longitudinally, but more in the anterior, and less in the lateral direction than in most fishes.

One cannot contemplate the relative position of the frontal to the parietal and of the parietal to the supraoccipital, which is overlapped by the parietal and itself overlaps the flattened spine of the atlas, without a conviction of the serial homology of these single, median, imbricated bones, all completing arches above the neural axis, and each permanently distinct from the piers or haunches of the arch of which it forms the key-stone. In like manner the serial homology of those piers or neurapophyses, viz. the laminæ of the atlas, the exoccipitals, the alisphenoids and the orbitosphenoids, is equally unmistakeable. Nor can we close our eyes to the same serial relationship of the postfrontals (fig. 20, 12, 12) as parapophyses of their vertebra, with the mastoids (8) and the coalesced paroccipitals (4). The frontal *parapophysis*, 12, is wedged between the back part of the spiue, 11, and the neurapophysis, 10: its outward process extends backwards and joins the next parapophysis (8); but, notwithstanding the retrogradation of the mandibular arch, it still receives a small part of its own *pleurapophysial* element (28). . This element now manifests its typical unity: vegetative subdivision, much reduced in the batrachian reptiles, no more prevails in the development of the frontal pleurapophysis in any higher vertebrate. The serpents exhibit this element under the common form of a rib; longer, indeed, than are any of the pleurapophyses in the batrachian order; but it has so far retreated in serpents as to be exclusively attached to the parietal parapophysis, which is remarkably elongated and produced backwards, and suspends the long, slender, straight and simple frontal pleurapophysis (tympanic pedicle) vertically from its posterior extremity. In lacertians no. 28 is vertically suspended from no. 8, and, commonly also, from no. 27, which is continued from the backwardly produced parapophysis of the frontal vertebra (12) to that of the parietal vertebra (8) in most of this division of the Cuvierian order *Sauria*. In chelonians and crocodilians the diverging appendage of the maxillary arch (27) descends and applies itself to a large proportion of no. 28, down to its lower articular end, and contributes to fix and strengthen that bone, as well as the modified costal arch from which it diverges.

The condition of the shortening, expansion and fixation of the frontal pleurapophysis in crocodiles and chelonians is exemplified in the uses to which the modified hæmapophyses, completing that costal arch, are put. Tortoises crop the grass by the application of the trenchant horny plates of the under to those of the upper jaw: turtles equally need a fixed suspensory joint of the under jaw in the act of biting and dividing the tough sea-weeds. Crocodiles have the frontal hæmapophyses (mandibular rami) unusually long; supporting numerous large laniary teeth, and requiring a fixed and firm point of suspension in the violent actions to which they are put in retaining, and overcoming the struggles of their prey.

The teleological complication of the lower or distal elements of the arch in question (29–32, fig. 22) is carried further than in fishes: there was more need, in fact, for a combination of the greatest elasticity and strength with the least weight of bone* in the frontal hæmapophysis of the crocodile than in the frontal pleurapophysis of the fish (28 *a*–28 *d*, fig. 5).

There, lastly, remain then in the skull of the crocodile the bones intersected by the lines N IV and the arrow H IV, with those numbered 26, 27, and 73, and we have to inquire whether through all the modifications which their extreme position subjects them to, we can still trace any evidence of their arrangement according to the vertebrate type.

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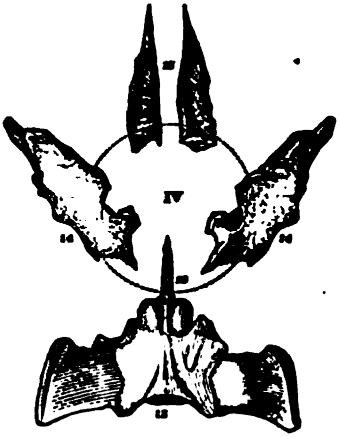
* Conybeare, Geol. Trans. 1821, p. 565. Buckland, Bridgewater Treatise, 1836, vol. i. p. 176. This author well illustrates the final purpose of the subdivision of the mandibular

A long and slender symmetrical grooved bone, like the ossified inferior half of the capsule of a notochord, is continued forwards from the centrum of the foregoing vertebra, and stands in the relation of a *centrum* (13) to the vertical plates of the bones 14, which expand as they rise into the broad and thick triangular plates with an exposed horizontal superior surface. The arch of which these form the piers, and to the anterior rhinencephalic prolongations traversing which arch they stand in the relation of *neurapophyses*, is completed by the two bones (15): which I, therefore, regard as a divided *neural spine*. In fishes we have seen that the corresponding element of the parietal vertebra was similarly divided, whilst the neural spine of the nasal vertebra was single: in the crocodile the reverse conditions prevail. In a species of alligator I have observed the bone 13 continued further forward, expanded, and divided at the middle line, the two divisions forming a small disc on the bony palate. The centrum of the nasal vertebra is divided longitudinally at the median line in batrachians, ophidians, and most lacertians; it is single in chelonians, but retains its cartilaginous state in some species (*Emys expansa, e.g.*). The neurapophyses (14, 14) transmit the olfactory nerves in all reptiles; but the ganglions are usually withdrawn backwards into the prosencephalic neural arch, leaving

Fig. 21.



Disarticulated rhinencephalic arch, with the anchylosed pterygoids (24) viewed from behind: Crocodile.

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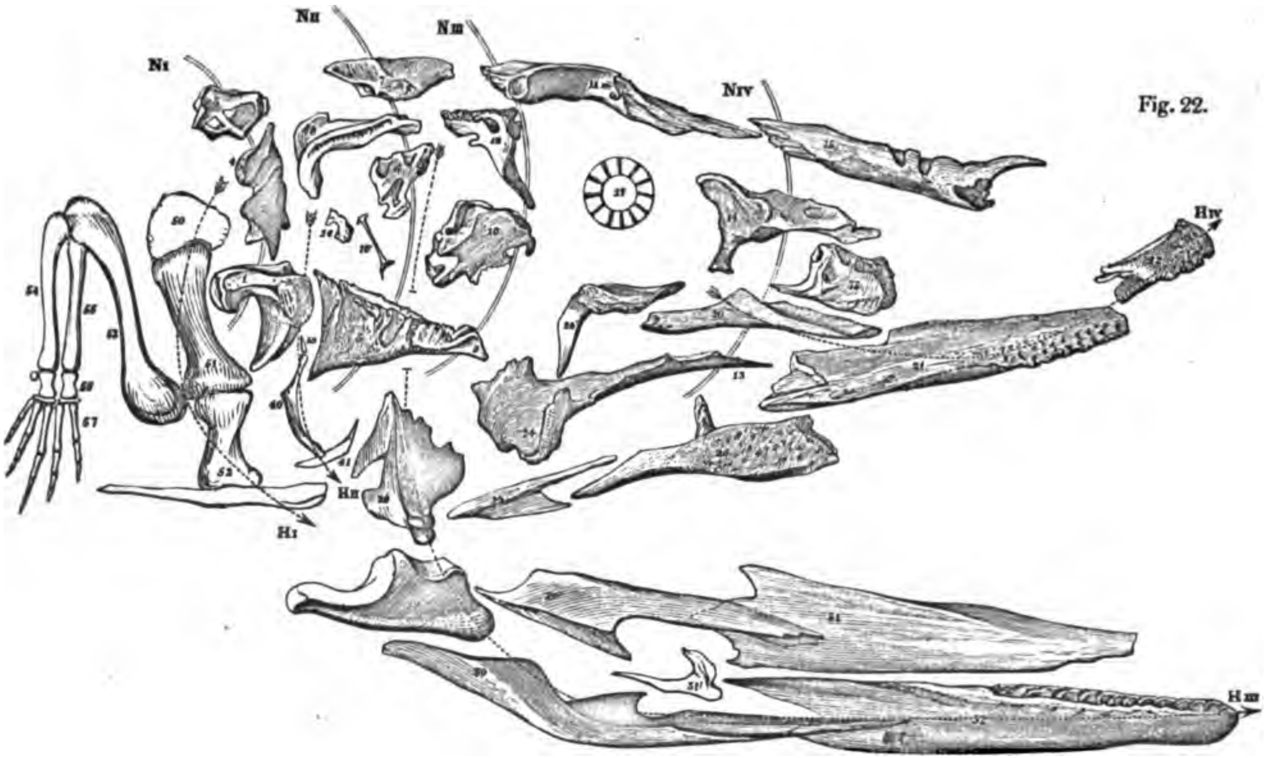
ramus in the recent and extinct saurians by pointing out the similarity of the structure to that adopted in binding together several parallel plates of elastic wood, or steel, to make a cross-bow; and also in setting together thin plates of steel in the springs of carriages. Dr. Buckland adds, "Those who have witnessed the shock given to the head of a crocodile by the act of snapping together its thin long jaws, must have seen how liable to fracture the lower jaw would be, were it composed of one bone only on each side."—*Ib.* p. 177. The same reasoning applies to the composite condition of the long tympanic pedicle in fishes. In each case the splicing and bracing together of thin flat bones of unequal length and of varying thickness affords compensation for the weakness and risk of fracture that would otherwise have attended the elongation of the snout. In the abdomen of the crocodile and plesiosaur the analogous composition of the hæmapophyses (abdominal ribs) allows of a slight change of length in the expansion and contraction of the walls of that cavity: and since amphibious reptiles, when on land, rest the whole weight of the abdomen directly upon the ground, the necessity of the modification for diminishing liability to fracture further appears. But what we are here chiefly concerned in is the evidence that the general homology of elementary parts of a natural segment is not affected by the modification of teleological composition of such parts. What happens to the hæmapophysial or inferior elements of the inverted arch in the abdominal segments of the crocodile also affects the same elements of a cranial hæmal arch; and the subdivision of the pleurapophyses of the trunk in the sturgeon is repeated in the same elements of the cranial vertebræ in osseous fishes.

only the nerve-trunks to be protected by the nasal neurapophyses. These are, therefore, more approximated, and the anterior termination of the neural canal is much contracted: and, in the tailless batrachia, the nasal neurapophyses coalesce together.

We recognise in that element (20) of the fourth or foremost inverted arch of the crocodile's skull, which is in connection with the body (vomer, 13) and descending plates of the neurapophyses (prefrontals, 14) of the nasal vertebra, the proximal or *pleurapophysial* element of such arch; and the same repetition of the characteristic connections of the bone, 20, which enabled Cuvier and Geoffroy to recognise its special homology with the palatine bone in the fish, establishes its claim to be equally regarded in the crocodile as the pleurapophysis of its vertebral segment; although it now affords but a partial attachment to the bone 21, which forms the next element of the inverted arch. This bone, the *hæmapophysis*, has undergone a striking change in its proportions by development both in length and breadth: it is connected not only with no. 20 behind and with no. 22 before, but with the elongated spine, no. 15, of its own vertebra, and with the lacrymals, 73, above; with its fellow of the opposite side below, and with a well-developed proximal element, no. 26, of a strong diverging appendage behind. The *hæmal spine*, no. 22, is divided, and the arch is completed by the symphysial junction of the two halves at H IV. The nasal aperture or entry to the air-passages forms the span or area of the much-modified inverted arch constituting the upper jaw of the crocodile. The two proximal elements of the arch, nos. 20 and 21, continue to send outwards and backwards exogenous diverging processes; but they constitute a smaller proportion of the bones than in fishes, and both processes directly support distinct bones representing the *diverging appendage* of the arch, and serving to fix and attach it to the succeeding arch. The pleurapophysial appendage (pterygoid, 24) soon coalesces, however, with its fellow and with the centrum of its own vertebra (vomer, 13), and then expands to unite by a broad sutural surface with the coalesced centrums of the frontal and parietal vertebræ (9 and 5). A second osseous piece (ectopterygoid, 24′) diverges from the pleurapophysis external to the preceding and attaches it to the hæmapophysis, to the hæmapophysial appendage, and to the parapophysis of the frontal vertebra. The strong diverging ray from the hæmapophysis is teleologically subdivided into nos. 26 (malar) and 27 (squamosal), and firmly attaches the maxillary arch to the pleurapophysis (28) of the mandibular one.

In the chelonian reptiles the modifications of the nasal segment of the skull adhere pretty closely to the type of those in the crocodile; the centrum is more independent and better developed, but the divisions of the neural spine have coalesced with their neurapophyses: the diverging appendages, 26 and 27, are usually developed into broad and flat bones. In many lizards we find the nasal centrum divided but the neural spine single: the hæmal spine is, also, single, as a general rule, and sends upwards and backwards a process to join the neural spine, divide the area of the hæmal canal, and terminate the vertebral series anteriorly. The hæmapophysial diverging appendage commonly resumes its long and slender ray-like proportions, and joins the parapophyses of both frontal and parietal vertebræ as well as the proximal end of the pleurapophysis of the mandibular arch. In serpents both divisions of this appendage are absent (indicating the inferior character of the bones 26 and 27 in general homology), but the two parts of the pleurapophysial appendage, 24 and 24′, are retained and serve as levers in the movements of the maxillary arch. The spine of that hæmal arch is single, and commonly united only by lax and elastic ligaments with the hæmapophyses,

Fig. 22.



Disarticulated bones of the neural arches (N I. to IV.) and sense-capsules, and of the hæmal arches (H to IV) and appendages, of the skull of the crocodile (*Alligator lucius*).

which may be divaricated like the halves of the mandibular arch, so as to widen the mouth laterally; and this free suspension and incomplete closure of the principal costal arches of the cranium in serpents repeats in an interesting manner the characteristic free and open condition of all the costal arches of their trunk. In the genus *Tythlops* the diverging appendage of the palato-maxillary arch is reduced to the primitive condition of a long and slender ray. In anourous batrachians a long and slender backwardly produced exogenous process of the hæmapophysis (maxillary) joins a shorter advancing exogenous process of the distal division of the next pleurapophysis (tympanic): but in the tailed species the maxillary arch is fixed only by a broad (pterygoid) appendage; and both maxillary and premaxillary retain only their essential connections as forming the inferior arch of their segment. In the proteus and siren the pleurapophysis (maxillary) is almost obsolete.

The bones nos. 24, 24', 26 and 27, being shown to be the least constant members of the group forming the nasal segment, and to form by their position and direction, the diverging appendages of the hæmal arch H IV, there remains in the skull of the crocodile only the bone 73, which by its position in front of the orbit and its relation to the lacrymal duct, is to be referred like the great anterior suborbital mucous bone in fishes to the dermal skeleton. In like manner the palpebral or supra-orbital scale-bones are to be excluded from the category of the pieces of the endoskeleton. The small and inconstant ossifications in the capsule of the organ of smell, together with the scarcely ossified sclerotals (17), the small petrosal, 16, and the columelliform stapes, 16', are intercalated portions of sense-capsules and appendages referable to the system of the splanchnoskeleton.

Thus the endoskeletal system of bones of the head of the crocodile are naturally arranged in four segments, each composed of a centrum with a neural and a hæmal arch. The hæmal arches have been subjected, as in the trunk, to most modification; that of the occipital vertebra having been displaced; that of the parietal vertebra detached from its segment and arrested in its development; whilst that of the frontal vertebra is articulated in a very small proportion to the parapophysis of its own segment, but chiefly to that of the parietal segment, with paroccipital connections also; it is immensely developed, the hæmapophysial portion being the chief seat of extension. The hæmal arch of the nasal segment is also very large, but shows as much excess of development in breadth as that of the frontal vertebra in length. The diverging appendage is more complex than in fishes: one piece indeed, no. 25, fig. 5, is absent, but three others, 24', 26 and 27, have been superadded. The diverging appendages of the frontal and parietal vertebræ cease to be developed in every class above that of fishes; but that of the occipital hæmal arch, though it no longer shows the luxuriant profusion of rays that distinguishes it in fishes, begins to assume a more fixed and definite character with more special powers and independent movements of its constituent parts. The first segment (53), doubtfully and obscurely recognizable in any fish, is henceforth a constant and important bone, and is always single: the next segment consists as exclusively of two bones, connate, indeed, in batrachians: the distal segment presents two jointed rays (digits) in the *Amphiuma didactylum*; three rays in *Amph. tridactylum* and the proteus and four rays in the *Siren lacertina*; it branched into as many as nine rays in the extinct ichthyosaurs; but they never exceed five in the existing saurians, which number is presented by this appendage in the crocodile (57, fig. 22.)

Birds.—The cranium of the bird offers the extremest instance of a homologically compound bone, and its development the clearest evidence of that principle of unity of composition which lies at the bottom of all the modifications of the cephalic division of the vertebrate endoskeleton. Although, as a general rule, the separate cranial bones can be discerned only at a very early period, yet in those birds in which the power of flight is abrogated the indications of the primitive centres of ossification endure longer, and in the species here selected for the illustration of the cranial segments (fig. 23) the constituent bones of the skull, though figured of their natural size, have, with the exception of the basioccipital, 1, and basisphenoid, 5, and the two bones, 6 and 8, which coalesce with the petrosal, 16, been separated by maceration merely. I may remark, however, that in all birds, certain bones, which coalesce with others in the cranium of most mammals, always retain their primitive individuality; the tympanic (28) and the pterygoid (24) for example.

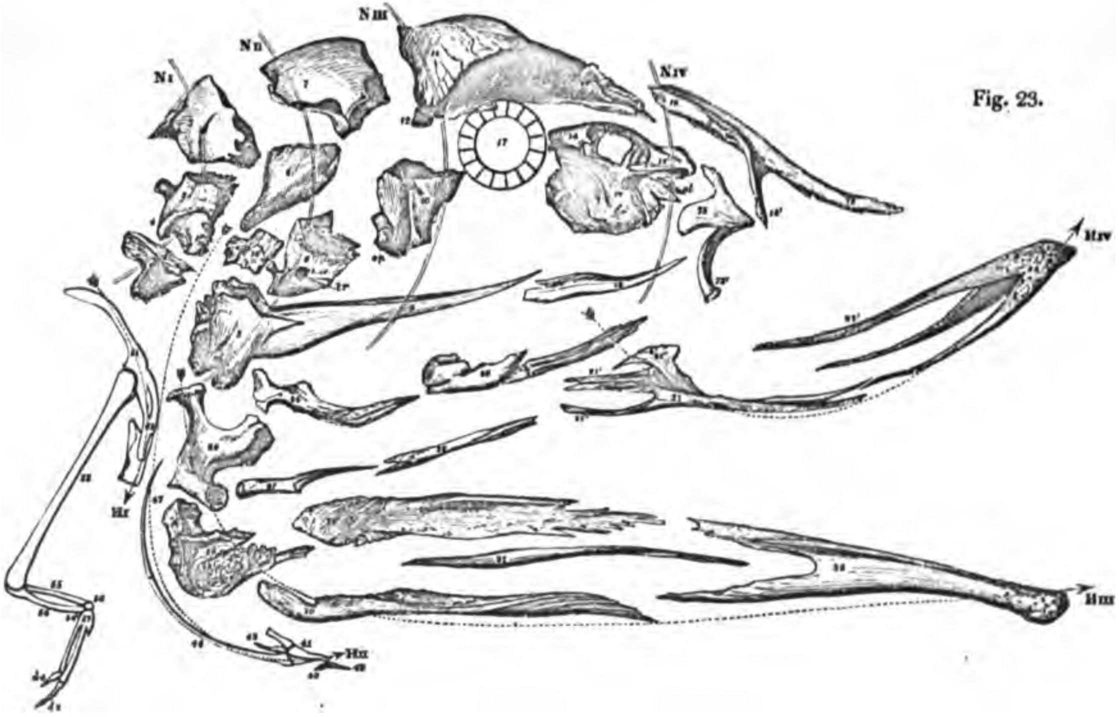
The hindmost segment of the cranium (N 1, fig. 23) so closely repeats the characters of the epencephalic neural arch of the crocodile (fig. 18), as to render a separate and full view of it unnecessary for the illustration of its vertebral character. The basioccipital (1) still developes the major part of the single articular condyle, and sends down a process, more marked in the struthious genera, and especially the dinornis, than in most other birds: in all respects this primitively distinct bone retains the character of the *centrum* of its vertebra.

The exoccipitals, 2, contributing somewhat more to the occipital condyle than in the crocodile, develope, as in that reptile, the paroccipital (4) as an outstanding exogenous ridge or process: but it is lower in position than in the crocodile: the proper *neurapophysial* characters of no. 2 are fully maintained. The supraoccipital (3) now begins to manifest more strongly the flattening and development in breadth, by which the spinous elements lose the formal character from which their name originated, and are converted from long into flat bones. We saw the first step in this most common of the changes to which one and the same endoskeletal element is subject, in the detached neural spine of the atlas of the crocodile: that of the occipital vertebra of the same animal presented another stage in the metamorphosis: we have a third degree in tha bird, and the extreme of expansion is attained in the human subject (fig. 25, 3), where the spine is sometimes developed, like that of the parietal vertebra, from two centres. But the arrested steps in this strange change of form and proportion demonstrate the essential nature of the part, as the neural arch, whilst the constancy of the characters of connexion is shown by this crown of the arch of the occipital vertebra having the exoccipitals as its piers or haunches from the fish to the human subject. It always protects the cerebellum; is absent in the frog where this organ is a mere rudiment; and is present in the crocodile in the ratio of the superior size of the cerebellum. The further development of the cerebellum is the condition of the superior breadth of the spine or crown of the epencephalic arch in the bird.

The arguments that determined the nature and displacement of the hæmal arch of the occipital vertebra in the crocodile apply with equal force to that in the bird. The extent of the displacement, it is true, has been greater: not seven, but seven-and-twenty vertebræ may intervene between the place of the scapulo-coracoid arch and the remainder of its proper segment constituting the occipital region of the simple cranial box in the bird. But this difference of extent ought no more to mask the real relationship of such costal arch to its centrum, than the degree of development of the spine of the occipital vertebra affects the general homology of that element.

In the ostrich, and other struthious birds, the hæmal arch of the occipital vertebra has retained much of its embryonic proportions. The *pleurapo-*

Fig. 23.



Disarticulated bones of the neural arches (N i to iv) and sense-capsules, and of the hæmal arches (H i to iv) and appendages, of the skull of the ostrich (Struthio camelus).

physial part (51) has, also, retained its slender rib-like form*; it has coalesced with the *hæmapophysis* (52), and the inverted arch is completed, as in the crocodile, by a hæmal spine, as much modified in form by flattening and expansion as is the neural spine represented by the supraoccipital (2). The diverging appendage of the occipito-hæmal arch also retains much of its primitive simple character: a long and slender bone (53) supports two rays (54, 55), and there is an attempt at three at 57, of which one is short, atrophied and anchylosed to the rest. In the two small bones (56, 56) interposed between this and the preceding segment, we recognise the special homologues of the carpal series in the crocodile and fish: in 54 we have the ulna, in 55 the radius, in 53 the humerus, in 57 the metacarpus; in *d* 3 and *d* 4 the rudiments of the digits so numbered in the crocodile (fig. 22) and the mammal (fig. 24). The evidences of the unity of plan in the construction of the scapular limb, whether it be an arm with the prehensile hand, a hoofed fore-leg, a wing, or a fin, are admitted by all; the same scapula, humerus, antibrachial, carpal, metacarpal and phalangial bones are readily recognised by the tyro in comparative osteology in the ape, the horse, the whale, the bird, the tortoise and the crocodile. The beautiful simplicity of the fundamental basis of all these adaptations of structure is descanted upon in all our popular teleological treatises. But the higher law governing the existence of these special homologies has attracted little attention in this country. Yet the inquiry into that more general principle of conformity to type according to which it has pleased the Creator of organic forms to restrict the manifestations of the variety of proportion and shape and substance and even relative position of the limbs requisite for the various tasks assigned to the vertebrate species, is one that by no means transcends the scope of the comparative anatomist. And the conclusion to which my comparisons have conducted me is, that one and the same element, viz. the diverging appendage of the occipital vertebra, forms in every case—to whatever adaptive modifications it may be subjected—the part recognized by the general term, 'anterior' or 'superior extremity.'

The second segment of the skull has for its *central* element a bone (fig. 23, 5), which in the bird, as in other ovipara, is connate with that (9) which stands in the same relation to the third cranial segment; the proof of the natural distinction of these segments is given by the neural, N II, N III, and hæmal, H II, H III, arches. Probably the circumstance of the bodies of those vertebræ being formed by ossifications of the fibrous capsule of the notochord, representing the external or cortical parts only of such centrums, may be the condition, or a favourable physical cause of such connation. The neural arch of the parietal vertebra retains the same characters which it first manifested in fishes. Besides the *neurapophyses* (6) impressed by the mesencephalic ganglia and transmitting the trigeminal nerves, besides the vastly expanded and again, as in fishes, divided neural spine (7), the *parapophysis* (8) is independently developed. It is of large proportional size; and, owing to the raised dome of the neural arch, is relatively lower in position than in the crocodile; it sends downwards and outwards an unusually long 'mastoid' process, and forms a large proportion of the outer wall of the chamber of the internal ear with the bony capsule of which it speedily coalesces.

The hæmal arch of the parietal vertebra (H II) is more reduced than in the crocodile, and owes much of its apparently typical character to the retention of the thyrohyals (46, 47) borrowed from the branchial arches of the visceral system, which are feebly and transitorily manifested in the embryo bird. These spurious cornua project freely or are freely suspended, and are the subjects of singular and excessive development, as has been exemplified in the chapter on Special Homology.

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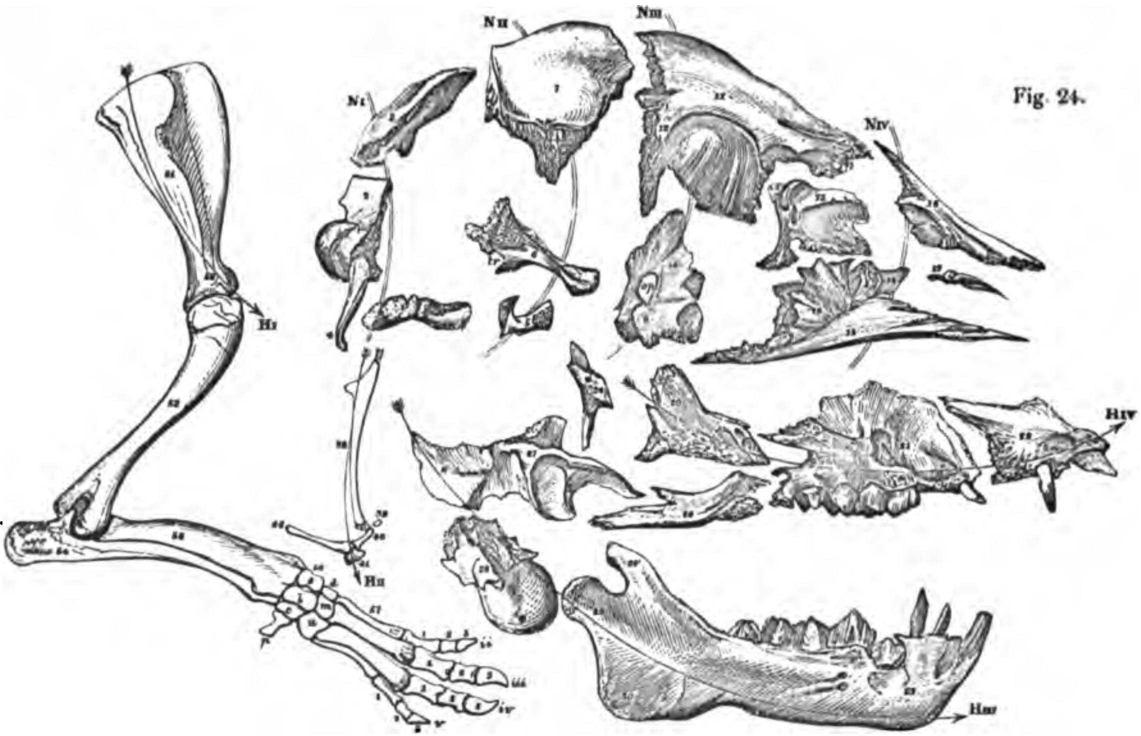
* The very common modification of form which this element undergoes in becoming expanded into the broad scapula of man and other mammalia, appears to have influenced Oken in his idea of that bone being the homologue of a congeries of ribs.

The bones (10) of the third neural arch protect a smaller proportion of the prosencephalon than in the crocodile, but maiutain their *neurapophysial* relation to it and to the optic nerves: the *neural spines* (11) cover a larger proportion of the hemispheres, and, with their homotypes (7), exhibit a marked increase of development in conformity with that of the cerebral centres protected by their respective arches. The *parapophysis* of the frontal vertebra (12) is relatively smaller in the bird than in the cold-blooded vertebrates, and is rarely ossified from an independent centre; but I have seen this in the emeu, and it appears to have been constantly an autogenous element in the dinornis. The hæmal arch of the frontal vertebra has been transferred backwards to the parietal one; its *pleurapophysis* (28), which is simple, as in the crocodile, articulating exclusively with the parietal parapophysis (8), though this in some birds unites with that of the frontal vertebra. In the young ostrich and many other birds traces of the composite character of the *hæmapophysis* are long extant; and bear obviously a homological relation to the teleologically compound character of the element in the crocodile: for the pieces, nos. 29, 30', *30'* and 31 ultimately, and in most birds early, coalesce with each other and with the *hæmal spine* (32), the halves of which are confluent at the symphysis.

The *centrum* (13) of the nasal vertebra is always single, and, when it does not remain distinct, coalesces with the neurapophyses, 14, and pleurapophyses, 20, of its own segment, and sometimes, also, with the rostral production of the frontal centrum (9): it is elongated and pointed at its free termination, and deeply grooved above where it receives the above-named rostrum; indicating by both its form and position that it owes its existence, as bone, to the ossification of the outer capsule of the anterior end of the notochord. In the ostrich the long presphenoidal rostrum intervenes between the vomer (13) and prefrontals (14). These latter bones manifest, however, as has been shown in the paragraph on their special homology (p. 214), all the essential *neurapophysial* relations to the rhinencephalon and olfactory nerves: but they early coalesce together, or are connate, as in the tailless batrachians. The *neural spine* (15) is divided along the middle line; but in most birds the suture becomes obliterated and the spine coalesces with its neurapophyses, with the frontal spine and with those parts of the hæmal arch of the nasal vertebra with which it comes in contact.

The *pleurapophyses* (fig. 23, 20) of this inverted arch retain their typical connections with the nasal centrum and neurapophyses at one end, and with the hæmapophysis (21) at the other end, and they also support the constant element of the diverging appendage of the arch, no. 24. The *hæmapophysis* (21) resumes in birds more of its normal proportions and elongated slender form: but the *hæmal spine* (22) is largely developed though undivided, and sends upwards and backwards from the part corresponding to the symphysis of the spine, when this element is divided, a long pointed process (22'), which joins and usually coalesces with the neural spine (15) and divides the anterior outlet of the hæmal canal into two apertures called the nostrils. The modification of the inferior arch of the nasal vertebra in the lizard tribe is here repeated. The pleurapophysial *appendage*, 24, connects the palato-maxillary arch with 25, and in the ostrich and a few other birds, also with *5*: the second or hæmapophysial ray of the diverging appendage is developed in all birds, as in the squamate saurians; combining the movements

Fig. 24.



Disarticulated bones of the neural (N I to IV) and hæmal (H I to IV) arches, and appendages, of the skull of a hog (*Sus Scrofa*).

of the hæmal arch of the nasal vertebra with that of the frontal vertebra, and consisting of the two styliform ossicles (26 and 27) which extend from the hæmapophysis, 21, 21″, to the pleurapophysis, 28: the essential relationship of the compound ray, 26 and 27, with the nasal vertebra, is indicated by their becoming confluent with its hæmapophysis (at 22″), whilst they always maintain an arthrodial articulation with the pleurapophysis (28) of the succeeding vertebra.

The bones of the splanchno-skeleton intercalated with the segments of the endoskeleton in the bird's skull are the petrosal (16), between the neural arches of the occipital and parietal vertebræ, early coalescing with the elements of those vertebræ with which it comes in contact: the sclerotals (17), interposed between the frontal and nasal neural arches: and the thyro-hyals (46, 47), retained in connection with the debris of the hæmal arch of the parietal vertebra, H II. The olfactory capsule remains cartilaginous. The dermal bone (73) is well-developed and constant: a second supraorbital dermal bone is occasionally present. All the endoskeletal bones manifest, under every adaptive modification, the segmental arrangement, and it is difficult to contemplate the disposition of the cranial bones in fig. 23, as in figs. 22 and 5, around the primary segments of the encephalon in the series of arches closed respectively by the bones N I, N II, N III, N IV, together with that of the corresponding number of arches closed below, at H IV, H III, H II and H I, without a conviction that the type illustrated in fig. 15 is that upon which these segments of the skull have been constructed. This conclusion might seem forced, in respect to the occipital vertebra, were its displaced hæmal arch and appendages to be viewed without reference to their relative position and connections in the lower vertebrate classes; but it will be confirmed and shown to be agreeable to nature and to the recognised kinds and grades of modification to which the elements of one and the same vertebra are subject, by observing in the young bird the distinct pleurapophysial elements of those cervical vertebræ, beyond which the corresponding elements of the occiput have retrograded, in obedience to the functions which the hæmal arch of that vertebra and its appendages are destined to perform in the feathered class.

Mammals.—If the foregoing views of the general homology of the bones of the skull be agreeable to their essential nature, we should expect that the new and additional modifications, in the mammalian class, which tend to obscure those relations would be seated in the appendages and peripheral elements of the endoskeletal segments, or in the capsules and appendages of the special organs of sense.

I have selected with the view to test such anticipation the skull of a young pachyderm*, and, after successively disarticulating the segments in the order in which they have been previously described, I have given a side view of them (fig. 24) arranged in correspondence with the figures 23, 22, and 5.

The neural arch of the occipital vertebra, N I, agrees with that of the bird and crocodile in the coalescence of the *parapophysis*, 4, with the *neurapophysis*, 2; but the process, 4, now descends from the lower part of the arch, and, as in many other mammals, is of great length. An articular condyle is also developed from each neurapophysis which articulates with the concave anterior zygapophysis of the atlas, and is the homotype of the posterior zygapophysis in the trunk-vertebræ. The centrum (1) is reduced, like that of the atlas, to a compressed plate, and its hinder articular surface is not more developed than is the front one of the centrum of the atlas, with which, indeed, it is loosely connected by ligament. The expanse of the occipital spine, 3, has been governed, agreeably with a foregoing remark, by the superior development of the cerebellum.

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* The skull of the ruminant is perhaps still better adapted to demonstrate the vertebral relations of the cranial bones: that of the sheep is the subject of the diagram for this purpose in the concluding volume of my 'Hunterian Lectures.'

The hæmal arch of the occipital vertebra is represented, like those of the cervical vertebræ, by the *pleurapophysial* elements only (51); but these, in most mammals, are developed into broad triangular plates with outstanding processes: that called 'spine' and 'acromion' is exogenous; but that called 'coracoid' is always developed from an independent osseous centre (a rudimental representative of the *hæmapophysis*, 52), which coalesces with the pleurapophysis in mammalia, and only attains its normal proportions, completing the arch with the hæmal spine (episternum) in the monotremes.

In many mammals the arch is completed by bones (fig. 25, 52'), apparently the hæmapophyses of the atlas, which have followed the occipital hæmal arch in its backward displacement, but not quite to the same extent.

The diverging appendage, though retaining the general features of its primitive radiated form, has been the seat of great development and much modification and adjustment of its different subdivisions (53–57) in relation to the locomotive office it is now called upon to perform.

With the exception of this excess of development of the appendage, the defective development and displacement of the hæmal arch, and the coalescence of the parapophyses in the neural arch, there are few points of resemblance which are not sufficiently salient between the segment N I, H I in the mammal, and that so marked in the fish (fig. 5). And, if the interpretation of the more normal condition of this segment in the lower vertebrate, according to the archetypal vertebra, fig. 15, be accepted, then the explanation here offered of the nature of the modifications of the special homologues of the constituents of the occipital segment by which that archetype is masked in the mammal, may be confidently left to be confirmed by the judgement of the unbiassed student of homological anatomy.

In commencing his comparisons of the second segment of the skull with the typical vertebra, he will be unexpectedly gratified by finding, in the immature mammal, the *centrum*, 5, naturally distinct, and the hæmal arch, H II, retaining its connections with the rest of the segment, and by means of a more complete development of the pleurapophyses (38) than in any of the inferior air-breathing vertebrates. He may now separate, without artificial division of any compound bone, the entire parietal segment, but he brings away with it the petrified capsule of the acoustic organ, and the anchylosed distal piece (27) of the maxillary appendage, which more or less encumbers and conceals the typical character of the neural arch of the parietal vertebra in every mammal: least so, however, in the monotremes and ruminants. The *neurapophyses* (6) of the parietal vertebra, like the mesencephalic segment of the brain, are but little more developed in mammals than in the cold-blooded classes: they are notched in the hog and perforated in the sheep by the larger divisions of the trigeminal, and they send down an exogenous process, which articulates and sometimes coalesces with the appendage (24) of the palato-maxillary arch. The *neural spine* (7), always developed from two centres, often vastly expanded, and sometimes complicated with a third intercalary or interparietal osseous piece, is occasionally uplifted and removed from its neurapophyses by the interposed squamous expansion of the bone 27; but this, which reminds one of the occasional separation of the neural arch from the centrum of the atlas in fishes, is a rare modification in the mammalian class. A still rarer one is the separation of the halves of the parieto-neural spine from each other by the extension and mutual junction at the median line of the occipital and frontal spines. A specimen of this, in a species of *Cebus*, which repeats the common modification of the parts in fishes, is preserved in the museum of the Royal College of Surgeons. The *parapophysis* (8) always commences as an autogenous element by a distinct centre of ossification, as shown in the human fœtus, fig. 11, 8; it speedily coalesces with the petrosal, but otherwise retains its individuality in some of the lower mammals, as *e.g.* in the echidna (fig. 12, 8): or it coalesces with the curtailed frontal pleurapophysis 28, or with the maxillary appendage 27, or with both these and the pleurapophysis of its own vertebra (38), when the complex 'temporal bone' of anthropotomy is the result. In most mammals the *pleurapophysis* (38) retains its primitive independency and rib-like form, with usually the 'head' and 'tubercle'; but by reason of its arrested growth it has been called 'styloid' bone or process. Sometimes it is separated from the short *hæmapophysis*, 40, by a long ligamentous tract, sometimes it is immediately articulated with it, or by an intervening piece. The *hæmal spine*, 41, is usually small, but thick and always single. The rudiments of hypobranchial elements (46) are retained as diverging appendages of the parieto-hæmal arch in all mammals, and have received the special names of 'posterior cornua,' or 'thyrohyals,' from their subservient relationship to the larynx.

In the frontal segment the *centrum*, 9, and *neurapophyses*, 10, very early coalesce. Two separate osseous centres mark out the body (fig. 26, C, 9), and each neurapophysis has two distinct centres (*ib.* 10, 10), the optic foramina (*op*) being first surrounded by the course of the ossification from these points. The superior development of the neurapophysial plates (fig. 24, 10), as compared with those of the parietal vertebra (6), in most mammals, harmonizes with the greater development of the prosencephalon; but the chief bulk of this segment of the brain is protected by the expanded spines of the frontal (11) and parietal (7) vertebræ, and by the intercalated squamosals (27). In many ruminants the bifid element 11 developes two spinous processes placed side by side as in the anterior trunk-vertebræ of the *Tetrodon*; but they project beyond the integument and are called 'horns.' The appendicular piece (27) not only usurps some of the functions of the proper cranial neurapophyses, but, likewise, the normal office of the frontal pleurapophysis (28), in the support, viz. of the distal elements of the hæmal arch (29, 32), which now articulate directly with 27, in place of 28 as in all oviparous vertebrates. The true *pleurapophysis* of the frontal vertebra (28) is almost restricted in the mammalian class to functions in subserviency to the organ of hearing, is sometimes swollen into a large bulla ossea, like the parapophyses and pleurapophyses of the cervical vertebræ of *Cobitis*, Pl. I, fig. 7, *pl*, *x*; it is sometimes produced into a long auditory tube, and sometimes reduced to the ring supporting the tympanic membrane. Yet, under all these changes, since its special homology is demonstrable with 28 in the bird (fig. 23) and crocodile (fig. 22) as well as with the teleologically compound bone, 28 *a*, *b*, *c*, *d*, in the fish (fig. 5), so likewise must its general homology, which is so plainly manifested in the fish, be equally recognised. The frontal *hæmapophysis* (fig. 24, 29, 30), and the corresponding half of the *hæmal spine* (*ib.* 32) are connate on each side in all mammals, and become confluent at H III, in most. The hæmal arch of the frontal segment of the skull, as in other air-breathing vertebrates, has no diverging appendage, unless the tympanic ototeals be so regarded, an idea which is not borne out by their development.

The nasal segment (N IV, H IV) is chiefly complicated by the confluence of parts of the enormously developed olfactory capsules (19) in the mammalian class, and its typical character is masked by the compression and mutual coalescence of the *neurapophyses*, 14. The *centrum* is usually much elongated, as at 13, and soon coalesces with both *neurapophyses* (14) and nasal capsules in the hog. The *neural spine* (15) is usually divided, but is sometimes single, *e. g.* in *Simia*. In the rhinoceros it supports a dermal spine or horn. The *pleurapophysis* (20) or proximal element of the hæmal arch of the nasal vertebra has its real character and import almost concealed by the excessive development of the second element of the arch (21), which resumes in mammals all those extensive collateral connections which it presented in the crocodile; and to which are sometimes added attachments to the expanded spine of the frontal vertebra, as well as to that of its own segment. The pleurapophysis however, besides its normal attachment to its centrum, 13, sends up a process to the orbit, in order to effect a junction with its neurapophysis which sometimes appears there, as the 'os planum' of anthropotomy. The *hæmal spine* (22) is developed in two moieties, which never coalesce together, although, in the higher apes, and at a very early period in man, each half coalesces with the hæmapophysis, and repeats the simple character of the corresponding elements (rami) of the succeeding (mandibular) arch.

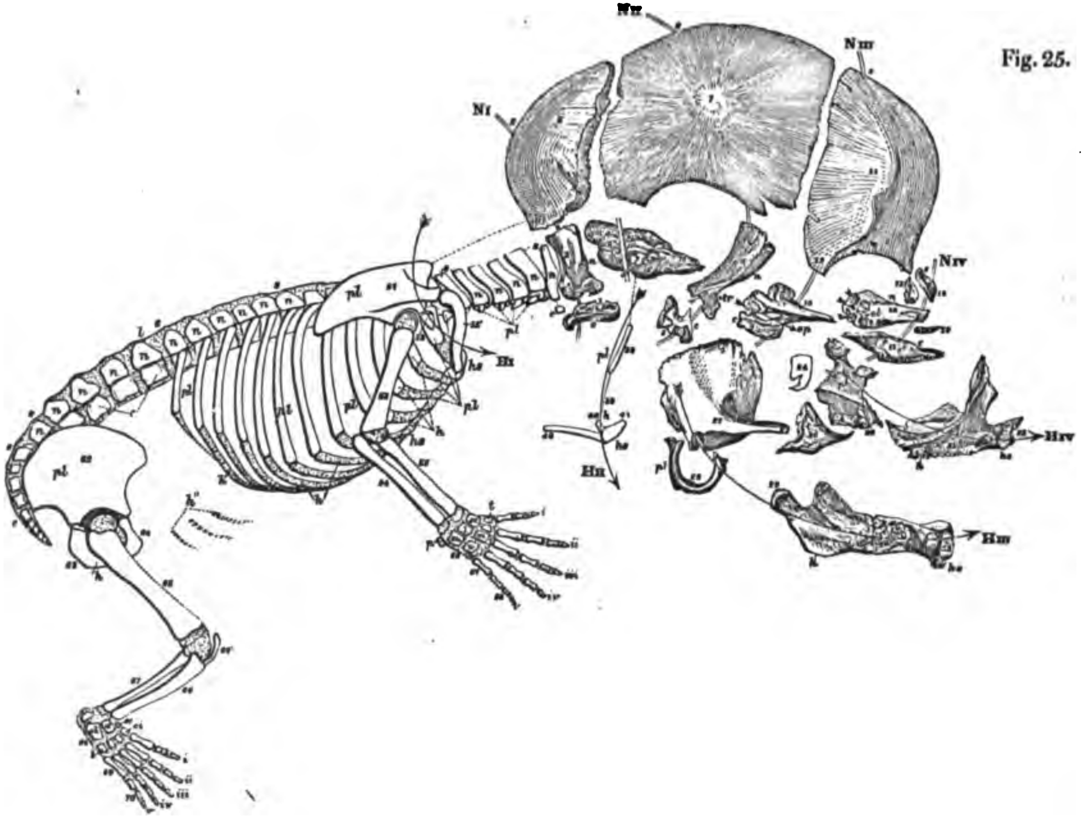
The *appendicular* element (24) which diverges from the pleurapophysis (20), contributes to fix and strengthen the palato-maxillary arch by attaching it to the descending process of the parietal centrum (5); with which, in most mammals, it ultimately coalesces. The other elements of the diverging member of the arch correspond in number and in the point of their divergence with those in birds, chelonians and crocodiles. They are two in number, succeeding each other, and both become the seat of that expansive development which is followed by the multiplication of their points of connection; thus the proximal piece ('malar' 26) articulates in the hog not only with the hæmapophysis (21) from which it diverges, but likewise with the muco-dermal bone, 73. The distal piece of the appendage (squamosal, 27) expands as it diverges, and fixes the naso-hæmal arch not only to the frontal pleurapophysis (28), but also to the frontal, parietal and occipital neurapophyses and spines: it also affords, in the hog, as in other mammals, an articular surface to the frontal hæmapophysis (28).

The development of an osseous centre in the cartilage of the snout of the hog, and the homologous 'prenasal' ossicle in certain fishes, the carp, *e. g.*, might be regarded as rudiments of terminal abortive segments more anterior than the nasal vertebra. The multiplied points of ossification in the vomer have been, also, deemed indications of that bone being, like the vomerine coccygeal bone in birds, a coalescence of several vertebral bodies. Of course, *à priori*, the segments in the cranial region of the endoskeleton might as reasonably be expected to vary in number in different species, as the segments in the thorrcic or sacral regions. I have not, however, been able to determine clear and satisfactory representatives of more than four vertebræ in the skull of any animal; and the special ossifications in the nasal cartilages appear to me to belong to the same category of osseous parts, as the palpebral bones in certain crocodiles and the otosteals.

Man.—Arriving, finally, in the ascensive survey and comparison of the archetypal relations of the bones of the vertebrate skull, at Man, the highest and most modified of all organic forms, in which the dominion of the controlling and specially adapting force over the lower tendency to type and vegetative repetition is manifested in the strongest characters, we, nevertheless, find the vertebrate pattern so obviously retained, and the mammalian modification of it, as illustrated in the preceding paragraph and diagram, so closely adhered to, as to call for a brief notice only of those developments of the common elements which impress upon the human skull its characteristic form and proportions.

The neural arch of the occipital vertebra differs from that of the hog by a much greater development of the *neural spine* (fig. 25, 3) and a much less

Fig. 25.



development of the parapophysis. This, as in other mammals, is not only an exogenous process of the *neurapophysis*, 2, but is commonly reduced to a mere "scabrous ridge extended from the middle of the condyle towards the root of the mastoid process" (Monro, *l. c.* p. 72)—the "eminentia aspera musculum rectum lateralem excipiens" of Soemmerring: the knowledge of its general homology, however, makes quite intelligible and gives its true interest to the occasional development of this ridge into a 'paramastoid' or paroccipital process, which now, however, projects, like the true 'mastoid,' downwards from the basal aspect of the cranium (*ante*, p. 30).

The occipital *pleurapophysis*, *pl*, *51*, shows the same displacement as in other mammals, but is still more expanded in the direction of the trunk's axis, and its exogenous (acromial) process is still more developed. The *hæmapophysis* (*52*), originally distinct, has its development checked and speedily coalesces with the pleurapophysis.

If the bone *52'* be the special homologue of the bone, *52*, Pl. I. fig. 2, in the fish,—and considering the backward displacement of *51* and *52*, its anterior position to them in man is no valid argument against the determination,—then we may adopt the same general homology, and regard the clavicle, in its relations to the vertebrate archetype, as the displaced hæmapophysial element of the atlas, to which segment its true relative position is shown in the same low organized class in which the typical position of the scapular arch is likewise retained.

The adaptive developments of the radiated appendage of the occipital hæmal arch reach their maximum in man, and the distal segment of the appendage constitutes in him an organ which the greatest of ancient philosophers has defined as the "fit instrument of the rational soul;" and which an illustrious modern physiologist has described "as belonging exclusively to man—as the part to which the whole frame must conform"*. And these expressions give no exaggerated idea of the exquisite mechanism and adjustment of its parts.

It is no mere transcendental dream, but true knowledge and legitimate fruit of inductive research, that clear insight into the essential nature of the organ, which is acquired by tracing it step by step from the unbranched pectoral ray of the protopterus to the equally small and slender but bifid pectoral ray of the amphiume, thence to the similar but trifid ray of the proteus, and through the progressively superadded structures and perfections in higher reptiles and in mammals. If the special homology of each part of the diverging appendage and its supporting arch are recognisable from Man to the fish, shall we close the mind's eye to the evidences of that higher law of archetypal conformity on which the very power of tracing the lower and more special correspondences depend?

Until the alleged facts (p. 117) are disproved, demonstrating change of position to be one of the modifications by which parts of a natural and recognisable endoskeletal segment are adapted to special offices, and until the conclusions (p. 118) deduced from those facts are shown to be fallacious, I must retain the conviction that, in their relation to the vertebrate archetype, the human hands and arms are parts of the head—diverging appendages of the costal or hæmal arch of the occipital segment of the skull†.

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* Bell (Sir Charles), "The Hand." Bridgewater Treatise, 1833, pp. 16, 18.
Μόνον δὲ καὶ ἀμφιδέξιον γίγνεται τῶν ἄλλων ζώων ἄνθρωπος.—*Aristotle.*

† As another example of the new light and interest which a knowledge of general homology gives to the facts of abnormal anatomy in the human species, I may cite the remarkable case described by Sir C. Bell (*op. cit* p. 52), of the boy 'born without arms,'—' but who had clavicles and scapulæ.' Here development was arrested at the point at which it is normal

The *centrum*, 5 *c*, of the parietal vertebra gives, in the human fœtus, the same evidence of its essential individuality, by the same absence of the mask of connation which somewhat concealed it in the oviparous classes, as we have already noticed in the lower mammal (fig. 24). The *neurapophyses* (6) rise higher to reach their proper *spine* (7) in the lofty cranial dome of man, of which that divided and enormously expanded element forms the greatest part of the roof: but the base of the neurapophysis continues to be perforated by the homologous divisions of the nerve (*tr*) that notches it in the cod-fish (fig. 5, 6 *tr*). The *parapophysis* (8) retains its autogenous or independent character in relation to its proper neural arch, the 'additamental' suture by which it manifests its normal relations to the neural spine (7) being persistent; but it speedily coalesces with the acoustic capsule, 16 (from which it is artificially separated in fig. 25), and with the modified *pleurapophysis*, 38, as has been already explained in the chapter on 'Special Homology' (Mastoid, pp. 29–42).

The proper *pleurapophysis* (38) of the parietal vertebra ordinarily becomes confluent with contiguous and coalesced portions of the parapophysis, 8, and acoustic capsule, 16; and the ossified portion of the *hæmapophysis*, 40 *h*, is separated from it by a long ligamentous tract, and becomes confluent with the *hæmal spine*, 41 *hs*. The entire inverted arch exhibits the usual arrested growth characteristic of the air-breathing vertebrates, and its appendages are represented by the still retained 'hypobranchial' elements, 46, of the splanchnic arches, which are so voluminously developed in the fish.

The *centrum* and *neurapophyses* (9, 10) of the frontal vertebra manifest the same speedy coalescence as in other mammals. The *spine*, 11, though developed from two lateral moieties, regains its normal unity, as a general rule, in man by the obliteration of the median suture: its transverse and vertical expanse here attain their maximum. The *parapophysis* (12) is developed, as in the occipital segment, as an exogenous process, called 'external angular or orbital' in anthropotomy, but from the neural spine instead of the neurapophysis. This element is perforated by its characteristic nerve (*op*). The *pleurapophysis*, 28, is now separated from its parapophysis, 12, by both parts, 27 and 26, of the diverging appendage of the maxillary arch; but yet it is interesting to note that it is still connected through the medium of these with the same element to which, agreeably with the greater retention of the vertebrate archetype, it directly articulates in the fish (fig. 5, 12, 28 *a–d*). The intercalated piece (27) further interposes itself, as in other mammals, between the pleurapophysis, 28, and hæmapophysis, 29, of the frontal segment, directly articulating with the latter and leaving the proximal element of the arch (28) reduced in man to its subordinate function of sustaining the ear-drum. The *hæmapophysis*, 29, and *hæmal spine*, 32, are connate, and soon coalesce with their

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in the *Anguis*, *Pseudopus*, and some other limbless and snake-like lizards. The usual predominating development of the scapular appendage has bred so prevalent an idea of the subordinate character of the supporting arch, that the existence of the arch minus the appendage, is adverted to not without a note of surprise in the above-cited and other excellent works. General homology, however, teaches that a vertebral arch is a more constant and important part than its appendages; and, that, being anterior in the order of development, it may be expected, in cases where development is arrested, whether normally in accordance with the nature of the species or abnormally as an individual defect, to be present when the diverging appendages are absent. Sir Charles Bell, well recognising the primary function of the modified occipital rib in relation to breathing, observes, in reference to the above-cited case, "We would do well to remember this double office of the scapula and its muscles, that, whilst it is the very foundation of the bones of the upper extremity, and never wanting in any animal that has the most remote resemblance to an arm, it is the centre and point d'appui of the muscles of respiration, and acts in that capacity where there are no extremities at all!" p. 52.

opposites at the symphysis menti; and the whole distal portion of the inverted arch of the frontal segment is then formed by a continuous bar of bone, modified in its form and articulation, and by its dental appendages, in subserviency to mastication and other functions in relation to the human mouth.

We recognise the *centrum* of the nasal vertebra in the human skull by the position and connections of the bone, 13, notwithstanding it has undergone as extreme a divergence from the ordinary cylindrical shape of such elements, as its homotype at the opposite extreme of the vertebral column in birds, which Cuvier compares to a 'soc-de-charrue': it is, in fact, more compressed and vertically developed than in the hog (fig. 24, 13); but it is shorter, and commonly retains its original individuality. It directly supports the similarly modified compressed and, also, coalesced *neurapophyses*, 14, which, terminating in like manner the series of their vertebral homotypes anteriorly, have undergone the extremest modification. But the arguments proving the coalesced prefrontals of the frog, the bird and the mammal to be the special homologues of the bones so called in the fish, establish, as a corollary, their general homology with those bones, which retain in so much greater a degree, and unmistakeably, their neurapophysial characters in that lowest class of cold-blooded vertebrates. The nature of the additional complication by which those vertebral or archetypal characters are further masked in mammals, has been already explained in relation to the nasal neurapophyses of the hog. The olfactory nerves are transmitted in man, as in that and most other inferior mammals, by numerous foramina, 14, *ol.* The *nasal spine*, 15, is divided, but much-restricted in its growth, and presents a singular contrast in that respect to its homotypes, 11, 7, 3, in the succeeding cranial vertebræ. The development of the neural arch of the nasal vertebra is so modified in man, so contracted as well as retracted, that the orbits, instead of being pushed apart and directed laterally, have approximated by a kind of reciprocal rotation towards the median plane, and have thus gained a directly anterior aspect.

General homology perhaps best explains the import of the continuation of the small and seemingly insignificant bones (20, *pl*) from the roof of the mouth "up the back part of the nostrils to the orbit," where they are connected "to the *ossa plana* and *cellulæ ethmoideæ* by the ethmoid suture." That the connection is the best possible for the functions of the bone we may feel assured, without the sentiment being damped by discerning in it, at the same time, the attempt to retain the type, and repeat those constant connections of the *pleurapophysis* in question, not only with its centrum (vomer), but also with the modified neurapophyses of its proper segment (prefrontals with coalesced olfactory capsules constituting the compound 'ethmoid bone' of anthropotomy). The connections of the pleurapophysis, 20, with its hæmapophysis, 21, in front, and its diverging appendage, 24, behind, are also retained in man; and in short, all those characters that, depending on the essential nature of the palatine bone as the pleurapophysis of its vertebral segment, have served to indicate its special homology from man to the fish, without doubt or difficulty, to all anatomists (see Table I.).

The *hæmapophysis* (21) has the usual mammalian expansion, but is unusually short in man, and coalesces unusually early with the corresponding moiety of the *hæmal spine* (22). Besides the normal and constant connections with 20 and 22, the hæmapophysis, 21, articulates with its fellow, with the centrum (13), neurapophysis (14, os planum), and spine (15), of its own vertebra, with the spine of the frontal vertebra (11), with the detached portion of the olfactory capsule (19), and with the muco-dermal bone (73). It also affords a large surface of attachment to the proximal piece of its diverging appendage (26), which, in addition to the more constant connections with 21 and 27, articulates in man with the neurapophysis (10) and parapophysis (12) of the frontal vertebra. The distal extremity of the second bone (27) of the diverging appendage attains its maximum of expansion in man, and besides its connection with 26, and the glenoid articulation for the hæmapophysis, 29, it joins the parietal neurapophysis, 6, and spine, 7, and sometimes also (in the melanian race) the spine (11) of the frontal vertebra: and it speedily coalesces with the reduced pleurapophysis, 28, of the frontal vertebra, and with the parapophysis (8) of the parietal vertebra, together with a portion of the capsule of the acoustic organ.

In reviewing the general characters of the human skull in reference to the vertebrate archetype, we find the occipital segment simplified by the atrophy and connation of its parapophyses and hæmapophyses; and modified chiefly by the excessive growth of its neural spine and pleurapophyses, and by the backward displacement of the latter element, as in all other air-breathing vertebrates. The parietal segment, retaining, like the occipital one, the more normal proportions of its centrum and neurapophyses, is still more remarkable for the vast expanse of its permanently bifid spine. As in most cold-blooded vertebrates, the parapophysis preserves its independence in respect of the neural arch of its own segment. The hæmal arch retains its almost fœtal proportions, but is less displaced than in some of the inferior air-breathing vertebrates. The primitive individuality of the centrum of the parietal vertebra is a feature by which the human subject, together with all other mammals, manifests a closer adhesion to type than is observable in this part of the skull in any of the oviparous vertebrates, and it shows the necessity of extending comparisons over the entire series, and not deducing the vertebrate archetype exclusively from those inferior forms: for although it may be upon the whole best retained in them, yet the modifications superinduced in subserviency to their exigences, and by which they diverge to that extent from the common plan, and, as a series of species, from the common vertebrate stem, may affect a part which the conditions of existence of higher forms do not require to be so masked. The early ossification and large proportional size of the hyoidean arch in the human embryo is very significant of its true nature and importance, in relation to the archetypal vertebrate structure, *i. e.* as being the hæmal complement of a primary segment of the skull.

Exogenous processes descend, like the pair from beneath the lower cervical vertebræ of some birds, from the body of the parietal vertebra; but the true transverse processes of this vertebra are the mastoids, which always articulate with a corner of the parietals.

The centrum and neurapophyses of the frontal segment retain their ordinary proportions, and the spine is again the element which, by its extreme expansion and its modification in subserviency to the formation of the orbits, chiefly masks the typical features of the neural arch. The parapophysis is connate and reduced in size, and its vertebral relations with the pleurapophysis of its segment interrupted by the interposition of the diverging appendage from the antecedent hæmal arch: the unusually expanded distal end of the same appendage also intervenes between the frontal pleur- and hæmapophyses; the pleurapophysis (28) being more atrophied in man than in most inferior mammals. The hæmapophysis and spine are on the other hand much developed and modified as above described, for the business of mastication, though relatively shorter than in other mammals.

The compression and extension, both vertically and longitudinally, of the centrum (13), the compression and coalescence of the neurapophyses (14), both with each other and the nasal capsules (18), and the corresponding proportions of the divided spine (15), mainly characterize the neural arch (N IV) of the terminal or nasal segment of the human skull. The early coalescence of each hæmapophysis (21) with the corresponding half of the divided hæmal spine (22), and the unusual expansion of the bones, especially the second (27), which diverge from the hæmapophysis, form the chief characteristics of the hæmal arch (H IV) of the nasal segment. The hæmapophysial portions of both the nasal and frontal vertebræ are much less elongated than in most other animals.

It may serve to test the accuracy of the general homologies here assigned to the bones of the human skull, if we notice the degree to which they have been subject to modification in connection with such determinations.

According to the general character of the vertebral elements in the rest of the frame, we should be prepared to expect that the hæmal arches would be subject to a greater variety in respect of development and relative position to their segments than the neural arches; and that in the latter the parts determined as centrums and neurapophyses would retain more of the ordinary proportions of such parts in other segments or in other animals, than the peripherally situated spines. If new bones are added, we should expect to find them in the relative position of appendages to the normal vertebral arches: or should these be homologous with similar superadditions in the skulls of lower animals, they will probably be the seat of more extensive changes of form, proportion and connections, than the elements of the vertebral arches themselves.

Now if the reader will glance at fig. 25 and compare the bones forming the segments of the skull with those in figs. 24, 23, 22 and 5, he cannot but be struck with the remarkable degree of uniformity in the dimensions of the bones 2, 6 and 10: no. 14 being the terminal neurapophysis, has been the seat of more variety; but the general steadiness of this series of bones in regard to their dimensions and connections accords with the characters assigned to them, as neurapophyses, which are always the most constant and important of the ossified vertebral elements.

The bones 1, 5, 9 and 13 equally conform in the kind and degree of their modifications with their determination as the bodies of the vertebræ.

The increasing capacity of the neural canal of the head, demanded for the lodgment of the progressively expanded encephalon as the vertebral scale rises, is chiefly acquired by the expansion of the bones, 3, 7, 11, which, being determined as 'neural spines' in the fish, might be expected to be subject to greater deviations from their typical form and proportions than the more central and essential parts of the neural arches. The terminal neural spine, 15, is subject to still greater varieties in the range of species, as might also be expected from its position. In one mammal, *e. g.* the porcupine, it is more expanded than any of its succeeding homotypes in the cranium; in man its proportions are so much reduced as greatly to mask the homotypal relation. In one mammal, *e. g.* the orang, the nasal spine is not only diminutive but single: in another mammal, *e. g.* the manatee, it is also diminutive but divided, and the halves completely separated by the intervention of part of the succeeding spine.

The abnormal conditions of the human skull give further illustration of the truth of these general homologies of the cranial bones, and reciprocally receive light from such determinations. In the case of idiots from defective growth or development of the brain, where the cavity of the cranium is reduced to half or less than half its normal capacity, as *e. g.* in the skull described and figured in my 'Memoir on the Osteology of the Chimpanzee*,' it might have been expected from the anthropotomical ideas of the cranial bones,—according to which no one bone is deemed either more or less important than another in its essential nature, and where the squamosal is as little regarded in the light of a superadded or intercalary piece as the alisphenoid,—that all would be reduced in the same proportion in forming the parietes of the contracted brain-chamber. But this is by no means the case. In the instance above-cited the basioccipital and basisphenoid have been developed to their usual size, and the distance from the posterior boundary of the bony palate to the anterior border of the foramen magnum is as great as in any normal skull. The exoccipitals (condyloid portions of the occiput), the alisphenoids and the orbitosphenoids retain in like manner their full dimensions. The distance between the frontal and temporal bones is as great as in the average of fully developed Caucasian skulls, and is greater than in most of those from the Melanian race, in which the direct junction of the frontal with the temporal, as in the chimpanzee, is by no means rare. The contraction of the capacity of the brain-chamber is due chiefly to arrested development of the frontals, parietals, supraoccipital and squamosals. By the reduction of the supraoccipital and the retention of the centrums of the cranial vertebræ of their normal proportions, the foramen magnum becomes situated nearer the back part of the basis cranii than in the normal skull.

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* Zoological Transactions, vol. i. p. 343, pl. 57 and 58.

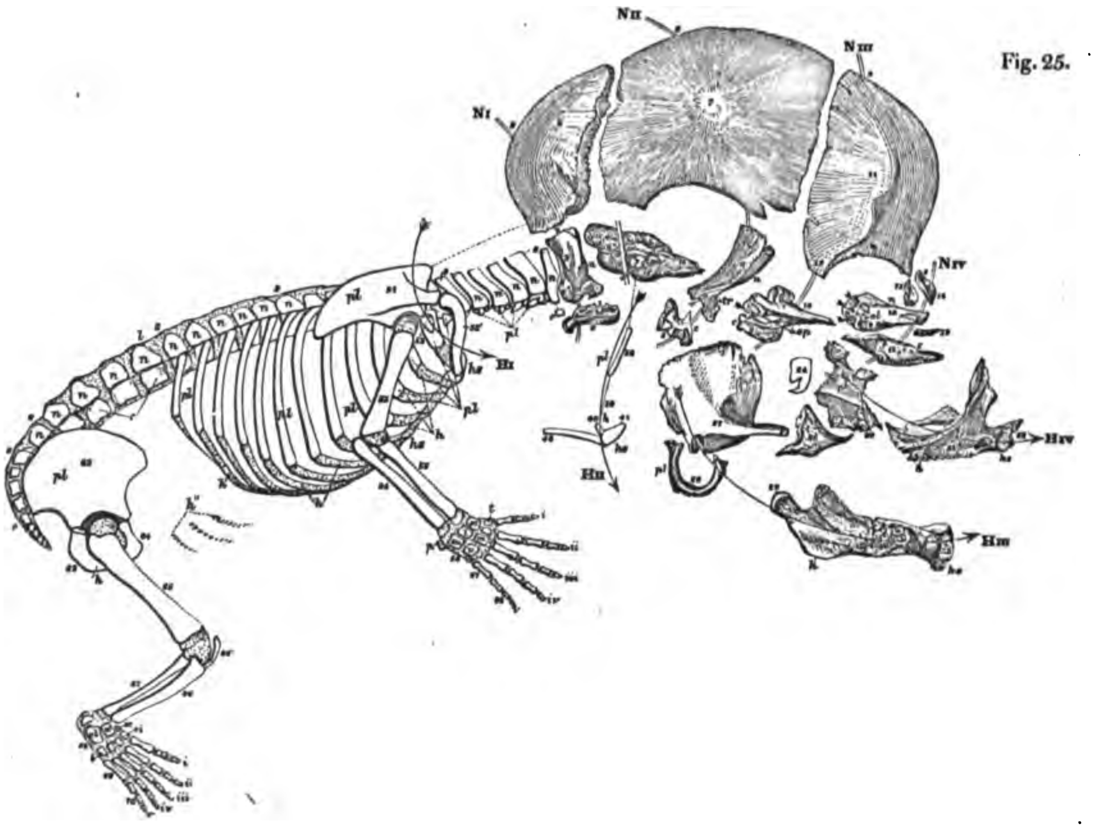
In a still smaller cranium of a female idiot, who reached the age of twenty-one years, which is preserved with the male idiot's skull above-mentioned in the anatomical museum of St. Bartholomew's Hospital, the contrast between the normal proportions of the basioccipital, basisphenoid, exoccipitals, alisphenoids and orbitosphenoids, on the one hand, and the reduced dimensions of the supraoccipital, parietals, frontals and squamosals on the other, is still more striking and significant of the true nature of those bones. The normal growth of the centrums, indeed, might be explained by the concomitant nearly normal size of the medulla oblongata, base of third ventricle and optic chiasma, in the brain of the same idiot: but it is not so obvious from the condition of the brain itself why the alisphenoid should not have shrunk in the same proportion as the parietals, frontals and squamosals. To the homologist, however, the recognised difference of subjectivity to modification presented by the neurapophyses, spines and diverging appendages of the typical segments, renders very intelligible the partial seats of arrested growth in the bones of these idiots' crania.

In reference to disease, also, one sees not why the alisphenoid should have a minor attraction for the morbid products deposited, or be less subject to the destructive actions excited, during syphilitic or mercurial disease, than the parietals, or the orbitosphenoids than the frontals, or the exoccipitals than the supraoccipital: yet it needs but to examine any series of such morbid skulls in our museums of pathology to be convinced that the variable and peripheral elements of the neural arches, viz. their expanded spines, are almost exclusively so affected: the frontal and parietal being the most common seats of the disease; the supraoccipital a less frequent one, concomitantly with its minor deviation from the typical standard of the element. I have yet seen no example in which either a cranio-vertebral centrum or neurapophysis was so affected; but the nasal bones are notoriously attacked.

It would be easy to multiply such instances of the new light—new eyes, so to speak,—with which human anatomy, normal and abnormal, is viewed, after the essential nature or general homology of the parts have been appreciated.

If the bones 4, 8, 12, fig. 5, have been correctly determined as the parapophyses of the cranial vertebræ, they might be expected to be subject in the

Fig. 25.



The course of coalescence reduces the epencephalic arch (fig. 25, N 1) to one bone, the scapular arch (H 1) to one bone (the arch is apparently completed by the connexion of an element (52') not appertaining to the skull). The centrums (5, 9) and neurapophyses (6, 10) of the parietal and frontal vertebræ coalesce with each other and with the diverging appendages (24) of the maxillary arch to form one bone, the 'sphenoid' of anthropotomy, and this ultimately coalesces with the epencephalic arch and constitutes the 'os spheno-occipitale' of Soemmerring. The expanded halves of the parietal spine (7) remaining usually distinct are reckoned as two bones. The expanded halves of the frontal spine (11) usually coalescing together form a single bone. The halves of the nasal spine (15) rarely coalescing are counted as two bones. The mastoid (8) coalescing with the petrosal (16) and this with the tympanic (28), squamosal (27) and stylohyal (38), the whole is reckoned a single bone, which thus combines a parapophysis and pleurapophysis of one vertebra with a pleurapophysis of another and a diverging appendage of a third vertebra, and all these parts of the endo-skeleton with a sense-capsule belonging to the splanchno-skeleton: such is the heterogeneous compound character of the 'temporal bone' of anthropotomy. The neurapophyses of the nasal vertebra (14) coalesce with each other and with a considerable part of another ossified sense-capsule (18), to form the single bone called 'ethmoid.' The maxillary bone includes the superior maxillary (21) and premaxillary (22) of the lower animals. The hyoid bone includes the basihyal (41), with the ceratohyals (40) and the thyrohyals (46). The scapula includes both the pleurapophysis (51) and the hæmapophysis (52) of the occipito-hæmal arch. The signification of the separate points of ossification of the human fœtal skull is made plain by the foregoing applications of the ascertained general homologies of the bones of that part of the skeleton.

Objections to the Cranial vertebræ considered.—The latest and most formal objection to the fundamental idea in accordance with which I have attempted to work out the general homologies of the bones of the head, is also the most formidable in respect of the great and deserved eminence of the objector. In a manuscript left by Baron Cuvier, entitled, "Le crâne est-il une vertèbre ou un composé de trois ou quatre vertèbres?" appended to the posthumous edition of the 'Leçons d'Anatomie Comparée*,' he admits that "the analogy of the basilar and two condyloid parts of the occiput with the body and two halves of the annular part of the atlas is very appreciable. The basioccipital and the body of the atlas serve equally to support the myelon; the exoccipitals and the two halves of the ring of the atlas to cover it. The condyles are represented by the articular processes by which the atlas is joined to the dentata. The condyloid foramen, which gives passage to the nerve of the ninth pair, has some relation with the hole in the atlas which gives passage to the first cervical nerve and to the first bend of the vertebral artery. Some have also found a certain relation between the mastoid process, which in most animals appertains to the occipital bone, and the transverse process of the atlas and the other vertebræ; upon which it murt be remarked that these relations are less in man, in some respects, than in the quadrupeds, since the atlas has commonly only a notch for the passage of the artery, and the mastoid belongs in man entirely to the petrosal"†. "We may even compare," Cuvier says, "the supraoccipital to the spinous processes which in certain animals originate by special points of ossification and remain for some time distinct from the rest of the vertebra: nevertheless, there is already here a great difference of structure and function [*]." With regard to the points in which Cuvier is willing to admit an 'analogy' between the occiput and the atlas, he subjoins, agreeably with his idea of the law which governed such correspondences,—"These resemblances might naturally be expected in the part of the head placed at the extremity of the vertebral column, and the functions of which are, in fact, analogous to those of vertebræ, since it gives passage, like them, to the great neural axis[†]."

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* Tome ii. p. 710. (1837) par MM. F. G. Cuvier and Laurillard, who hold the arguments of their author to be conclusive. The criticism in the 'Histoire des Poissons,' t. i. p. 230, bears only upon the *à priori* cranio-vertebral theory of Geoffroy, and does not concern us here.

† "L'analogie de ces trois pièces, le basilaire et les deux condyloïdiens, avec les trois pièces de l'atlas, son corps et les deux moitiés de sa partie annulaire est très sensible. Le basilaire et le corps de l'atlas servent également à supporter la moëlle épinière; les condy-

With regard to the feature of resemblance (quelque rapport) which some had seen between the mastoid process and a transverse process, Cuvier founds his objection to its application to the vertebral character of the occipital bone on a false homology. Concluding that the mastoid in man (fig. 25, 8) was homologous with the paroccipital in the hog (fig. 24, 4)[‡] and some other quadrupeds, he deems the determination of the paroccipital as the transverse process of the occipital vertebra to be invalidated by the fact that the 'mastoid' belongs, in man, not to the occipital but to the petrosal. There were cases, however, not unknown to the able Editors of the posthumous edition of the 'Leçons d'Anatomie Comparée,' where the true transverse processes of the occipital vertebra, though exogenous like those of the succeeding trunk-vertebræ in man, had become developed to an equal extent with such transverse processes; the abnormality of the human occipital thus repeating its normal condition in the quadruped. They however do not cite these instances, or notice the confusion by their author of the true mastoid with the paroccipital in reference to this his first objection to the vertebral homology of the occipital segment. But it might further have been remarked, in respect of the segment of the skull to which the mastoid really stands in parapophysial relation, that although the mastoid belongs in man to the petrosal in the sense of being anchylosed with it, it articulates with the parietal; and the persistence or obliteration of a primitive suture is too variable a phænomenon to determine to which of two bones a third connected with both essentially belongs. The constant existence of the paroccipital either as an autogenous element or an exogenous transverse process in all the oviparous vertebrate classes, its common existence in mammals, and occasional, though rare, development in man, establish that additional, though by no means essential vertebral character in the occipital segment, which

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loïdiens et les deux moitiés de l'anneau de l'atlas à la couvrir. Les condyles sont représentés par les facettes articulaires au moyen desquelles l'atlas s'unit à l'axis. Le trou condylien qui laisse passer le nerf de la neuvième pair, a quelque rapport avec le trou de l'atlas qui laisse passer le premier nerf cervical, et la première courbure de l'artère vertébrale. On a aussi trouvé quelque rapport entre l'apophyse mastoïde qui, dans la plupart des animaux, appartient à l'occipital, et l'apophyse transverse de l'atlas et des autres vertèbres; sur quoi il faut remarquer que ces rapports sont moindres dans l'homme à certains égards que dans les quadrupèdes, puisque l'atlas n'y a ordinairement qu'une échancrure pour le passage de l'artère et que l'apophyse mastoïde y'appartient entièrement au rocher."—*l. c.* p. 710.

[*] "On pourrait même comparer l'occipital supérieur aux apophyses épineuses qui, dans certains animaux, naissent par des points d'ossification particuliers, et restent quelque temps distincts du reste de la vertèbre; cependant il y aurait déjà ici une grande différence de structure et de fonction."—*l. c.* p. 711.

[†] "Ces resemblances étaient naturelles à attendre dans la partie de la tête placée à l'extrémité de la colonne vertébrale, et dont les fonctions sont en effet analogues à celles des vertèbres puisqu'elle laisse passer comme elles le grand tronc medullaire."—*l. c.* p. 711.

[‡] Cuvier, *e. g.* describes this element as "L'apophyse mastoïde, qui est très-longue, très-pointue et toute de l'occipital," in his elaborate *Ossemens des Cochons*, Oss. Fossiles, t. ii. pt. i. p. 117.

Cuvier seeks to obscure by the normal absence of its proper transverse processes in man, and the assumed transference of them to another part of the skull.

Cuvier in the next place objects to the comparison of the supraoccipital with the neural spine of a trunk-vertebra, "because of its vast difference of structure and function." He does not specify the nature of the difference: he admits that the neural spines have distinct centres of ossification in certain animals; and all will allow that, in most of the trunk-vertebræ of such, the neural canal is closed by the coadapted ends of the neurapophyses to which the spine articulates or becomes anchylosed: that therefore such spine does not directly cover the neural axis, but, retaining the shape signified by its name, performs exclusively the function in relation to muscular attachments. At first view the contrast seems conclusive against all homology between such mere intermuscular spine and the broad thin convex plate applied over the cerebellum and posterior cerebral lobes in man. And it must be confessed that the determination of their general homological relations could not have been satisfactorily demonstrated by the mere relations of the parts to the laminæ supporting them, in so limited a range of comparison. But, if we descend to fishes, we shall find the supraoccipital often equally excluded from the neural canal by the meeting of the exoccipitals beneath its base; we shall, also, see it still retaining the spinous figure, indicating its function in relation to muscular attachments to predominate over that in subserviency to the protection of the epencephalon. If we then ascend to the crocodile, we shall find the neural spine of the atlas to be one of those examples alluded to by Cuvier, where the ossification proceeds from an independent centre: and it not only thus manifests its essential character as an autogenous vertebral element, but maintains its permanent separation from the neurapophyses: and it further indicates the modifications of form to which the corresponding elements will be subject in the more expanded neural arches of the antecedent cranial segments by having already exchanged its compressed spinous for a depressed lamellar form. Here indeed Cuvier might not only have objected to recognise it as a vertebral spine by reason of its change of form and function, but also by its continuing a distinct bone, which is not the case with the expanded 'spine' of the mammalian occipital vertebra. But returning to the crocodile, we observe in the segment anterior to the atlas that both the form and connections of the supraoccipital (fig. 22, *3*) are so closely similar to those of the neural spine of the atlas that the recognition of their serial homology is unavoidable; and we have a repetition of the same characters of the vertebral element in question in the small and undivided parietal (*ib.* *7*). Now Cuvier makes no difficulty in admitting the 'occipital supérieur' in the crocodile to be the homologous bone with its more expanded namesake in the bird; or this with the still more expanded 'partie grande et mince de l'occipital' in mammals and man: he is also disposed to admit the special homology of the supraoccipital under all its variations of form and function in the above-cited air-breathing animals with the bone *3* in fishes, which he sometimes calls 'occipital supérieur,' sometimes 'interpariétal.' If then the special homology be admitted on the ground of the constancy of the connections of the part, with what show of reason can its general homology be rejected which forms the very basis or condition of the characters determinative of such admitted special homology? But Cuvier is not consistent with himself in his grounds of objection to the essential nature of the human supraoccipital as the neural spine of its segment; for he does not hesitate to call the atlas of the crocodile a vertebra, although its 'annular part' is closed above by a transverse plate* instead of by a vertical spine, of which, indeed, there remains hardly more vestige than is presented by the tubercle or rudiment of the spinous process in the supraoccipital of man. It must also be remembered, that the human supraoccipital does retain to a certain extent the same function in relation to the attachment of the proper vertebral muscles (*splenii capitis*, *complexi*, and the modified interspinales called '*recti capitis postici maj. et min.*) as the succeeding vertebral spines; and combines this with the same place of completing, as the key-stone, the neural arch; although by reason of the more voluminously developed segment of the neural axis protected by that arch the peripheral element is chiefly modified for the acquisition of the required increase of space.

Cuvier next proceeds to comment on Oken's endeavour to represent the basisphenoid and the two alisphenoids with the two parietals as forming a vertebra: and he admits that there is some analogy, though this is much more feeble than the differences. "The basisphenoid, having another function, takes on a different form from the basioccipital, especially above, by virtue of the posterior clinoid processes: and in the embryo it is composed not of a single nucleus, but of two†." With respect to the objection from the modification of form alluded to, it may be remarked that the same element in other vertebral segments of the body undergoes much greater change of shape; the centrums of the lower cervical vertebræ in many birds send down two processes as well-marked as the ascending ones called 'clinoid' in that of the parietal vertebra, not to speak of the 'soc de charrue' of the coccygeal vertebræ of the bird, for example, without any difficulty having been felt or expressed by Cuvier in their recognition as modified vertebral bodies, the more essential characters of their general homology being as plainly retained as in the case of the basisphenoid; in its relation, *e. g.* to the neurapophyses and the support of the mesencephalon. With regard to the objection from the two centres of development, if this be valid against the general homology of the basisphenoid (*s*, fig. 25) as a vertebral centrum, it equally tells against the body of the atlas (*c*), which, as Cuvier well knew, was ossified sometimes from two, and sometimes from three centres‡. And I may further observe that, although Cuvier affirms the two ossific centres of the basisphenoid to retain for a long time between them simple cartilages, my observations bear out the accuracy of the remark of Kerkringius, (whose figures Cuvier cites,) touching the "dua ossicula distincta" (tab. xxxiv. fig. iii. *c*, *c*), viz. "quæ celerrimè in formam figuræ appositæ K coalescunt": and the figure of the coalesced rudiments of the basisphenoid given by Kerkringius closely resembles the bilobed rudiment of the vertebral centrums in the sacrum of the chick.

Cuvier next objects to the neurapophysial character of the alisphenoids, that the 'foramen ovale' is rarely a notch, more often a complete hole.

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* "*Les vertèbres.* L'atlas est composé de six pièces, &c.—La première, *a*, est une lame transverse qui fait le dos de la partie annulaire. Elle n'a qu'une crête à peine sensible pour toute apophyse épineuse."—Ossemens Fossiles, t. v. pt. ii. p. 95.

† En avant du basilaire se trouve le corps du sphénoïde postérieur, aux côtés duquel adhèrent les deux ailes temporales ou grandes ailes. On a aussi cherché à représenter ces trois pièces comme formant une vertèbre avec les deux pariétaux. Il reste en effet encore quelque analogie, mais beaucoup plus faible, tandis que les différences deviennent plus fortes. Le corps du sphénoïde a bien l'air d'une répétition du basilaire, mais ayant une autre fonction il prende aussi une autreforme, surtout en dessus, au moyen des apophyses clinoïdes postérieures; et dans les premiers temps du fœtus il n'est pas composé d'un seul noyau, mais de deux, qui ont long-temps entre eux de simples cartilages."—*l. c.* p. 712.

‡ Leçons d'Anat. Comparée, t. i. (1836) p. 174. Meckel has figured the variety of three ossific centres in this element of the human atlas in the 1st vol. of his Archiv für die Physiologie, taf. vi. fig. 1.

"Now," he urges, "vertebræ properly so called give passage to the nerves only by the intervals that exist between them and the other vertebræ, and not by particular foramina[*]." Therefore the young anatomist must conclude that the dorsal vertebræ of the ox, the abdominal vertebræ of the lophius, and every other segment of the trunk whose neural arches are directly perforated by the spinal nerves, are to be rejected from the vertebral category!

It has been shown in the generalities on the corporal vertebræ (p. 95), that the neurapophyses in relation to the passage of their governing nerves may be either untouched, notched or perforated by them, without prejudice to their neurapophysial character. Viewed in the entire series of vertebrata the cranial neurapophyses are more frequently perforated than notched, those of the trunk more frequently untouched or notched by the nerves in passing through their interspaces.

The penetration and sagacity of Cuvier nowhere shine forth more brightly than in his bold and true determination of the bone *a*, fig. 5, in the cod-fish[†] as the homologue of the temporal wing of the sphenoid in the human skull. To any less-gifted comparative anatomist the relation would have been masked by the coalescence of the homologous part in man, by its connections with the squamosal and frontal, and its comparatively small proportions under the guise of a subordinate process; none of which characters exist in the alisphenoid of fishes: it still retains, however, in that class, as in man, its most essential connections in relation to the bones of its own segment and to the brain and nerves; and Cuvier availing himself of these in the determination of its special homology, was little likely to be swayed by so unimportant a variety as the transmission of the characteristic nerve by a foramen instead of by a notch. No sooner, however, has the time arrived and the call been sounded for an advance to a higher generalization, which includes and explains the minor proposition, than Cuvier interposes the least important difference of the alisphenoid to check the progress. It will be obvious to the anatomist that the foregoing explanation of the value of the nerve-notch or hole in the homological character of a neurapophysis has been called forth by the weight of the name of the objector rather than by the force of the objection.

Cuvier directs his next argument against the vertebral character of the (neural arch of the) parietal segment generally. "Its composition," he avers, "is different from that of other vertebræ, since the ring (he had just before denied its annular form) would be composed of five pieces or even of six, including the interparietal." Yet Cuvier does not hesitate, in his Article V., '*Les Vertèbres*' (Ostéologie des Crocodiles)[‡], to reckon as the first vertebra, the atlas notwithstanding its composition of six pieces.

If, indeed, Cuvier had subscribed to Geoffroy's assertion, that "Nature reproduces the same number of elements, in the same relations, in each vertebra, only she varies indefinitely their form,"—his objection to the vertebral character of any given segment that might deviate from the assumed normal number of pieces would have been intelligible. But even, then, he would not have been guided consistently by his own principle; for the objection founded upon the supposed abnormal number of pieces in a cranial segment weighs

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[*] "Ses ailes diffèrent beaucoup plus encore et des deux condyliens, et des deux pièces qui forment la partie annulaire des vertèbres. A la vérité, le trou ovale n'est quelquefois qu'une échancrure; mais le plus souvent il est entouré d'os, et par conséquent un vrai trou. Il en est de même du trou rond toutes les fois qu'il est distinct du sphéno-orbitaire; or les vertèbres proprement dites ne laissent passer les nerfs que par les intervalles qui existent entre elles et les autres vertèbres, et non par des trous particuliers."—*l. c.* p. 712.

[†] Règne Animal, 1817. pl. viii. fig. 2, *e*, p. 184.

[‡] "L'atlas est composé de six pièces qui, à ce qu'il paroît, demeurent pendant toute la vie distinctes."—Ossemens Fossiles, t. v. pt. ii. p. 98.

not at all against the recognition of a corresponding segment of the trunk, though similarly composed.

In fact, throughout this attack upon the vertebral theory of the skull, it will be seen that it is based upon the *à priori* assumption that all the endoskeletal segments of the trunk, however modified, are vertebræ, and all those situated in the head, are not vertebræ. The essential character of a vertebra is thus deduced from its position, not its composition. It needs only to compare any of Cuvier's objections to the vertebral character of the cranial segments, with the modifications of the corporal segments admitted by him to be vertebræ, previously enumerated in this Work (pp. 96–101), to see that the characters of the cranial vertebræ objected to by Cuvier differ in degree not in kind, and become valid arguments against the admittance of natural segments into the vertebral category, only when they happen to be situated at or near the commencement of the series.

It has been abundantly proved, I trust, that the idea of a natural segment (vertebra) of the endoskeleton, does not necessarily involve the presence of a particular number of pieces, or even a determinate and unchangeable arrangement of them. The great object of my present labour has been to deduce, by careful and sufficient observation of Nature, the relative value and constancy of the different vertebral elements, and to trace the kind and extent of their variations within the limits of a plain and obvious maintenance of a typical character.

In reference to the neural arch, the variation in the number and disposition of its parts, illustrated in the figures 1, 2, 3, 4, 18, 19, 20, 21, do not seem to me, nor will they I apprehend to any unbiassed anatomist, to obliterate the common typical character of that part of a vertebra. Those elements which are furthest from the centrum are the chief seat of the changes. If the reader will compare figure 2 with figure 19, he will see for example that the crown of the arch is formed by a single bone(*7*) in the crocodile, but by two bones (*7*, *7*) in fish; nay, in most fishes the halves are even pushed apart by the interposition of a third bone. Yet the sagacity of Cuvier led him to determine the divaricated moieties of the divided parietal in such fishes to be the same (homologous) bone with the single parietal of the crocodile. With what consistency, then, can the general homology of the segments be rejected, which suffer no other change in their composition than that resulting from the single or bifid character of the same bone in each? Is the single frontal of the human adult regarded as a distinct bone from the bifid frontal of the fœtus? If, therefore, the neural arch of the parietal vertebra (mesencephalic arch) of the crocodile be free from the objection, raised by Cuvier to the vertebral character of the homologous arch in man, on the score of the number of its elements; neither can that objection be allowed to have any force when it rests upon the mere division in the human mesencephalic arch of the recognised homologue of the single spinous element in the crocodile.

In the sheep, the arch which encompasses the epencephalon is formed by only three elements, the neural spine resting upon the conjoined upper ends of the neurapophyses. In the dog these elements are divaricated and the epencephalic arch is closed above by the neural spine. Now Cuvier does not allow this difference of arrangement of the latter element (*3*) to affect his recognition of the 'suroccipital' in both mammals; and, therefore, one is at a loss to discover the consistency of the ideas which would repudiate the general homology of the bones or of the entire arches which they surmount, because, as Cuvier would say, "the composition of the arch is different, being of three pieces in the sheep and of four pieces in the dog." Yet this is precisely the kind of objection which he has directed against the mesencephalic arch, viz. because it may be composed of five or even six pieces, in certain animals. In the fish, in fact,—by reason of the parietal parapophyses (8, 8) being subject to the same variation in their relative position to the other elements, which has been illustrated in respect of the neural spine in the epencephalic arch of the dog and sheep,—the mesencephalic arch is composed of seven pieces, or, including the interposed supraoccipital, of not less than eight bones. Yet even here we clearly and easily trace the kind and degree of modification to which the fundamental plan of the neural arch has been subject. The archetype is nowise obliterated: the general homologies of the modified elements are not less recognisable than their special homologies. The centrum and neurapophyses are the steadiest elements: the spine is not only subject to great diversity of size and shape, but to some variety of position, and, moreover, to be either single or bifid: the parapophyses have less range of variety in point of dimensions, but may be more or less interposed between spine and neurapophyses, or may become confluent with either element. Thus the epencephalic arch of the crocodile (fig. 18) differs essentially, in a Cuvierian sense, from that of the tortoise or the fish (fig. 1), because it is composed of four pieces in the first and of six pieces in the latter; the difference of composition merely depending, however, on the more exterior position and connation of the parapophyses, 4, 4, in the crocodile.

The independency of the parietal and frontal bones is next urged by Cuvier as militating against the idea that they complete a vertebral arch formed respectively by the alisphenoids and orbitosphenoids as the piers or haunches: and the more so, inasmuch as they are separated from those bones in some animals by the intercalation of the squamosals*. By parity of reason we must reject the general homology of the neural arch and spine of the atlas in the *Silurus* (Pl. I., fig. 3, *n a*), *Ephippus* and some other fishes, because that part of the vertebra is not only distinct, but uplifted and removed from the piers or base of the arch by the intercalation of the articular processes of the neural arches of the occiput and axis. According to Cuvier such separated atlantal arch must be regarded as a new bone, and the centrum ought therefore equally to be viewed as 'une pièce particulière qui a une destination particulière': but the general homology of vertebral elements may be determined not only by the irrelations to their own segment, but by those which they maintain with their less modified homotypes in contiguous segments.

The centrum of the atlas in the *Ephippus* directly sustains other neurapophyses than its own, and so far has a new or particular function; but, since it continues to unite the centrum of the axis with that of the occiput, we still regard it as their homotype, and as standing in the relation of the centrum to its uplifted and shifted neurapophyses. So, likewise, although these elements now aid in strengthening the joint between the zygapophyses of the neural arches of the occiput and axis, and thus perform a new and very peculiar function, their relation to these and other neural arches in the series of vertebræ renders it impossible to overlook the serial homology of the separated 'laminæ' of the atlas and that of its spine with the other and larger vertebral laminæ and spines.

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* "Dans tous les cas, on ne pourrait regarder cette vertèbre comme annulaire, ni supposer que les pariétaux en forment le complément; d'une part, ce serait une composition différente de celle des autres vertèbres, puisque l'anneau serait formé de cinque pièces et même de six, en comptant l'inter-pariétal; de l'autre, il arrive dans plusieurs animaux que les ailes temporales du sphénoïde n'atteignent pas au pariétal, parceque le temporal va toucher au dessus d'elles, soit au frontal soit au sphénoïde antérieur. Ainsi les pariétaux sont des pièces indépendantes du sphénoïde postérieur, des pièces particulières qui ont une destination particulière, celle de servir de bouclier à la partie moyenne et postérieure des hémisphères, tout comme les grandes ailes ont celle de servir de support aux lobes moyens dans lesquels ces hémisphères se terminent vers le bas."—*l. c.* p. 712.

The new functions which the uplifted and independent spines of the parietal and frontal vertebræ perform in man and many mammals are, with respect to the parietal bones, to shield the upper surface of the middle and posterior parts of the cerebral hemispheres, whilst the frontal is confined to covering the anterior lobes of the same hemispheres.

Hereupon it may be asked whether such relations and offices are the rule or only the exception; and, if the latter, whether it occurs in the lowest or the highest of the vertebrate series; whether in that class where the archetypal arrangement of parts is most, or in that in which it is least departed from? All these considerations are felt to be indispensable by the homologist in quest of the true signification of the parts of the animal frame, before drawing his conclusions from the first modification that may present itself. They are neglected by Cuvier in the objection to the vertebral character of Oken's 'kiefer-wirbel,' founded upon the relations which the parietal bones present to the encephalon in the mammalian class. Yet the more normal relations of those bones, both to the encephalon and to the alisphenoids, seem to have been present to the mind of Cuvier, and to have been duly appreciated by him when he defined, in 1817, the second cranial cincture as constituted by the parietals and sphenoid*.

With regard then to the first of Cuvier's arguments for viewing the human and mammalian parietals as 'des pièces particulières qui ont une destination particulière,' viz. that they are separated from the alisphenoids by the temporal bones. If we commence our consideration of it by the question, whether this separation be the rule or the exception, the reply which Nature sanctions will be that they are not so separated in any of the three great classes of oviparous vertebrata, nor in the majority of mammalia, nor even, as a general rule, in man himself. With regard to the second objection founded on the interposition of the enormously and backwardly developed prosencephalon between the mesencephalic spines (fig. 25, 7) and the mesencephalic segment of the brain, to which the parietal vertebra essentially relates,—its value will depend on the choice made by the homologist between the function of the parietals as immediate shields to the optic lobes (mesencephalon) in the cold-blooded classes, and their function as mediate ones through the interposed mass of the hemispheres (prosencephalon) in the warm-blooded classes, as that which best manifests adhesion to the ideal archetype. What to me has ever appeared one of the most beautiful and marvellous instances of the harmony and simplicity of means by which the One great Cause of all organization has effected every requisite arrangement under every variety of development, is the fact, that the protection of the enormous cerebrum peculiar to the higher mammals has not been provided for by new bones—by bones, *e. g.* developed from centres so numerous or so situated as to render any determination of their homologies as vague and unsatisfactory as would result from the attempt to determine those of the dermal ossifications upon the head of the sturgeon, in reference to the endoskeletal epicranial bones in fishes and reptiles. We might well have expected, had conformity to type not been a recognizable principle in the scheme of organized beings, to have had so many 'particular bony pieces' and so situated in the expanded human cranium as would have baffled all our endeavours to reduce them to the type of the epicranial bones of the reptile or fish. Yet the researches of the great comparative anatomists of the present century, and more especially those of Cuvier himself, have proved that there is no such difficulty: and a glance at the Table of Special Homologies, No. 1, will show that the bones (3, 7, 11) most modified in relation to the expanded cerebrum and cerebellum of man and mammals are

* Règne Animal, i. p. 73.

precisely those of which the determination has been easiest, and respecting the names and nature of which there has been the least discrepancy of opinion. It is with pain and a reluctance, which only the cause of truth has overcome, that I am compelled to notice the inconsistencies into which the great Cuvier fell, when his judgement became warped by prejudices against a theory, extravagantly and, perhaps, irritatingly, contended for by a contemporary and rival anatomist. After having established by the clearest evidence and soundest reasoning in his great and immortal works that the bones (7) in the fish (figs. 2 and 5) and reptiles (figs. 9, 10, 13, 19, 22) were homologous with those in birds (7, figs. 8 and 23), mammals (7, figs. 12 and 24), and even in man (7, figs. 11 and 25); and, after contending that they ought to bear the same name—under which, indeed, we find him describing them in the 'Leçons d'Anatomie Comparée' from man down to the fish—Cuvier comes at last to declare that, in those animals in which they are separated from the alisphenoids and mesencephalon, they are "particular pieces which have a particular destination!"

The relation of the mastoids (8, 8), as parapophyses, to the parietal or sphenoidal vertebra not having been detected in Cuvier's time, he supposes that the pterygoids, in the system which makes a vertebra of the sphenoid, can be compared to nothing else than the transverse processes of such. As, according to my views, they are recognizable in General Homology as quite distinct elements of another cranial vertebra, the arguments which Cuvier advances in disproof of what he thought they must be called, do not concern the subject of the present Report. The inferior exogenous processes, indeed, of the basisphenoid in mammals are not unlike those developed from the under surface of the centrum of the atlas in *Sudis gigas*, or from some of the cervical centrums in birds. The argument founded by Cuvier on the autogenous development of the true pterygoid (figs. 24 and 25, 24) would weigh little against its parapophysial nature, if other characters concurred to prove it a 'parapophysis;' but its connections and position show it to be a 'diverging appendage.'

With respect to the anterior sphenoid, Cuvier affirms that its composition is totally different from that of the posterior sphenoid and occipital, and from that of any vertebra. By the term 'sphénoïde antérieure' is meant the coalesced presphenoid and orbitosphenoids (figs. 24 and 25, 9 and 10); and the two bones referred to in the comparison signify, the one, the basi- and alisphenoids (*ib.* 5 and 6), and the other the basi- and ex-occipitals (*ib.* 1 and 2). With respect to the bone 9 and 10, Cuvier remarks that it is never, in mammals, formed of three pieces, but only of two; and that these are properly the rings for the optic nerves, which in course of time approximate and coalesce with each other: but so long as the median suture divides them, no distinct or third bony nucleus is developed in the intervening cartilage*.

Since, however, we see that the homologues (recognised as such by Cuvier) of the orbitosphenoids are something more than rings surrounding the optic nerves in the bird (figs. 8 and 23, 10) and crocodile (figs. 9 and 22, 9)—that they are merely notched by the optic nerves, and are chiefly developed in neurapophysial relation to the sides of the prosencephalon,—we are led to carry our inquiries into an earlier period of their development than that adduced by Cuvier, as contravening their vertebral characters. Cuvier cites the figure 2, in pl. xxxv. of the 'Osteogenia Fœtuum' of Kerkringius, as evidence of his statement of the developmental characters of the 'sphénoïde antérieur." That figure, however, exhibits the condition of the bone, when, although the median suture remains, each orbital ala has become anchylosed with the posterior sphenoid, and is likewise directly perforated by the optic nerve. The gelatinous cells of the anterior extremity of the notochord very early retrograde to the basioccipital region of the basis cranii, and the notochordal capsule alone is continued to the anterior extremity of the basis. This is converted into cartilage, and the osseous particles which ultimately constitute the anterior sphenoid are deposited as follows: first a centre or nucleus appears, in each orbital ala, external to the hole by which the optic nerve passes through the primitive cartilage (fig. 26, A, 10); soon after a second nucleus (*ib.* B, 10) is established at the inner or mesial side of each optic foramen: these centres form the foundation of the neurapophyses or orbitosphenoids, and ultimately coalesce around the optic nerve, as Kerkringius has depicted. But a third pair of ossific centres (*ib.* C, 9) is established behind the optic foramina between these and the baispshenoid (5). This third pair unite together into a single transverse bar (*ib.* D, 9), before coalescing with the orbitosphenoids in front, or with the basisphenoid behind, and that bar transitorily represents the centrum of the frontal vertebra. To the objection that such supposed centrum is developed from two points instead of one, the same reply may be made that was made before to a similar objection raised by Cuvier against the general homology of the basisphenoid; which objection, as was then shown, would be equally valid against the universally admitted homology of the body or centrum of the atlas.

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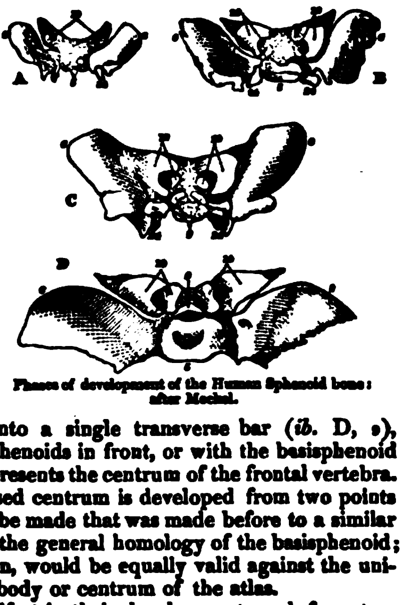
* "L'on a voulu aussi considérer le sphénoïde antérieur comme une vertèbre dont les frontaux compléteraient la partie annulaire, et où la position du trou sphéno-orbitaire entre les deux sphénoïdes repondrait assez aux trous inter-vertébraux ordinaires. Mais la composition du sphénoïde antérieur lui-même est toute différente de celle des deux os, dont nous avons parlé avant lui, et de celle d'aucune vertèbre. Il n'est jamais, dans les mammifères, formé de trois pièces, mais seulement de deux; ce sont proprement des anneaux osseux pour les nerfs optiques, qui par suite du temps se rapprochent et se soudent entre eux; la suture est toujours au milieu, et tant que l'ossification n'est pas complète, il n'y a entre les deux anneaux que du cartilage, dans lequel il ne se forme pas de troisième noyau."—*l. c.* p. 714.

Fig. 26.



Phases of development of the Human Sphenoid bone: after Meckel.

The frontal neurapophyses manifest in their development, each from two centres (fig. 26, B, C, 10), a transitory mark of vegetative repetition analogous to that which permanently characterizes the neurapophyses of the trunk-vertebræ in the sturgeon and, perhaps, the frontal neurapophyses themselves in the fishes with the bone 9′, fig. 5, Pl. I.

Thus the evidence of development, when complete, tells for, rather than against the serial homology of the 'sphénoïde antérieur' of Cuvier with the centrum and the neurapophyses of other vertebræ; and the more obvious and important characters of relative position to the other bones of their own segment, and to their homotypes in the contiguous segments, as well as to prosencephalic segment and characteristic nerves,—which characters have served to determine the special homologies of the coalesced bones in question (9, 10) from man down to the fish,—concur with the developmental characters in establishing the general homology of the presphenoid as centrum and of the orbitosphenoids as neurapophyses of the frontal vertebra.

Cuvier affirms, however, in support of his argument, that, although the orbitosphenoids are never separated from the frontals, as the alisphenoids are from the parietals, in the mammalia, they are almost always separated from the frontals in the other classes, so that the vertebral ring is again interrupted *. But, were even the frontals commonly uplifted above the orbitosphenoids in birds, reptiles and fishes, which does not accord with my experience, the objection, on that score, to regarding them as 'neural spines,' would as little apply, as it does to the universally recognised general homology of the separated and uplifted neural arch of the first vertebra of the trunk of the *Silurus* (Pl. I, fig. 3), *Ephippus* and some other fishes.

Cuvier finally regards the connection of the frontals with the prefrontals, which he calls 'ethmoid' in mammals, 'l'enchâssement de l'ethmoïde,' as a function quite remote from any of a vertebral character, "relative à toute autre chose." This objection only shows the necessity of a right appreciation of special homologies, in order to form a true judgement respecting general homology; and, with respect to the 'ethmoïde,' I must refer to the section on the prefrontals in the chapter on 'Special Homology (p. 46). If the arguments there adduced be held to prove the crista galli and cribriform plate in the human skull to be the homologues of portions of the coalesced prefrontals and olfactory capsules, we may next remark that these portions are not merely wedged between the orbital plates of the frontal, but articulate behind by a persistent suture with the orbitosphenoids. As neurapophyses, the coalesced prefrontals of the terminal vertebra of the skull thus articulate with their next succeeding homotypes; and, by virtue of the excessive development of the spine of the frontal vertebra, as well as from their being contracted and drawn backward in the human skull, they articulate with such spine (the frontal) as well as with that of their own proper segment (the nasals). But, in the crocodile (fig. 9), we have seen a similar relation manifested not only by the more normal neurapophyses (14) of the nasal vertebra, but likewise by those (10) of the frontal, those (6) of the parietal, and those (2) of the occipital vertebra.

All the objections raised by Cuvier to the general homology of the cranial bones as modified vertebral elements, equally apply to elements of vertebræ in the trunk, which Cuvier himself has admitted to be vertebræ, notwithstanding such modifications. The repetition of the perforated character of the human alisphenoid and orbitosphenoid in the neurapophyses of the trunk-vertebræ of many inferior animals, requires only a passing notice. The flattening, expansion and sutural union of the human supraoccipital, parietal and frontal bones, are matched by the neural spines in the carapace of the tortoise. If the basioccipital, basisphenoid and presphenoid are broad and flat, instead of cylindrical, so likewise are the bodies of the sacral vertebræ in the broad-bodied megatherioids and in many birds. If the basioccipital and basisphenoid are lengthened out and firmly united together by deeply indented sutural surfaces in most fishes, so likewise are the bodies of the four anterior vertebræ of the trunk in the pipe-fish (*Fistularia*, Pl. I., fig. 6). If the basisphenoid and presphenoid be developed each from two ossific centres, as in man, so likewise may the body of the human atlas be ossified; and even should the moieties of that centrum not coalesce at the median plane, they

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* "Ce que j'ai dit des pariétaux s'applique aux frontaux, considérés comme compléments du sphénoïde antérieur; leur fonction est relative à toute autre chose, à la protection des lobes antérieurs du cerveau et à l'enchâssement de l'ethmoïde; et quoique le sphénoïde antérieur n'en soit jamais séparé dans les mammifères comme le postérieur l'est souvent des pariétaux, il l'est presque toujours dans les autres classes, en sorte qu'alors l'anneau vertébral serait aussi interrompu."—*l. c.* p. 714.

would nevertheless still retain their essential characters as divisions of a single vertebral element: just as does the vomer in the salamanders, salamandroid fishes and serpents, which begins to be developed from two lateral points, like the body of the human atlas occasionally, without the development ending, as it always does in such atlas, by confluence of the resulting halves. It would be more reasonable to repudiate the general homology of the body of a whale's dorsal vertebra with the centrum of the typical vertebra, because it consists of three pieces set end to end, than to deny the general homology of the vomer because it may consist of two pieces set side by side, or that of the anterior trunk-vertebræ of the silurus because they consist of two pieces set one upon the other (Pl. I., fig. 3, *c a*, *e a*, *e x*, &c.). These are examples of a principle of variation which Cuvier never permitted to blind his perception of the special homology of certain bones, the mandibular ramus, for example; though vegetative or teleological subdivision is carried out to a much greater extreme there than in any vertebral centrum; unless, indeed, the number of points from which the whale's vomer be ossified may equal those in the crocodile's lower jaw. But if the differences in this developmental character, viz. of ossification from a single ossific point as in the vomer of the cod, or from two points as in that of the lepidosteus, or from three or more points as in the human vomer, interpose no obstacle to the determination of the special homology of the bone is from man to fish, it can as little avail as an argument against its general homology, which is determined not by the development of the vomer but by its relations to the other constituents of the segment of the skeleton to which it naturally belongs.

The great difficulty which the anthropotomist may naturally experience in forming an idea of the vomer as the body of a vertebra, will arise from its extremely modified form in the human subject: but he must bear in mind that it is an extreme part, the last of its series counted forwards; and if he should desire some higher and better established authority than the present Work before yielding assent to the vertebral character of the bone, under its characteristic 'ploughshare' mask in man, I know no name more influential than that of Cuvier himself, in regard to the equally and similarly modified centrum at the opposite end of the vertebral series in the bird. For although the mask of coalescence is superadded to that of strangeness of shape in the bone which Cuvier there compares to a ploughshare [vomer, or 'soc de charrue'], the great anatomist and cautious generalizer does not hesitate to affirm that it is "composed of many vertebræ" (see *ante*, p. 95).

It may, perhaps, be said that the coccygeal vomer must be vertebral in its nature because it is situated in the tail; but the 'petitio principii' in this argument will be transparent, if we transpose the locality, and say that 'the cranial vomer must be vertebral in its nature because it is placed in the head.' For what are 'head,' 'tail,' 'thorax,' or 'pelvis,' but so many diversely modified portions of a great segmental whole? These localities do not determine the nature of the segments composing them; such knowledge can only be acquired by a study of the composition of the segments; and it is the modifications of the segments that determine the nature of the localities or divisions of the endoskeleton, to which such special names as 'head,' 'thorax,' &c. are applied.

Yet Cuvier himself, perhaps, little suspected how much his ideas of the essential nature of a segment of the endoskeleton were governed by the part of the body in which it happened to be placed. Whenever the young anatomist finds a difficulty from the peculiar form or development, division or coalescence, of a cranial bone, in recognising or admitting its vertebral character, let him compare the results of his own observations with those summed up in pp. 96–101, and see whether the same kind of modification may not be repeated in the homologous element of a vertebra of the trunk in one or other of the species of vertebrate animals.

The latest direct objection to the cranio-vertebral system is from the pen of the celebrated ichthyotomist of Neuchatel. M. Agassiz represents the current ideas respecting this system at the period when he published his objections to it, in the following graphic passage of his invaluable and splendid work:—"It was M. Oken who had printed the first programme on the signification of the bones of the skull. The new doctrine which he set forth was received with extreme enthusiasm in Germany by the school of Naturalists called 'Natur-philosopher.' The author at that time required three cranial vertebræ, and the basioccipital, the sphenoid and the ethmoid were viewed as the central parts of these cranial vertebræ. Upon these pretended bodies of vertebræ were raised the arches enveloping the central parts of the nervous system (our 'protective plates'); whilst to the opposite side were attached the inferior pieces which should form the vegetative arch destined to embrace the intestinal canal and the great vessel (the 'facial arches' of which we shall presently speak). It would be tedious to enumerate here the changes which each author has rung upon this theme in modifying it agreeably with his notions. These contented themselves with the number admitted by Oken; those raised the number of cranial vertebræ to four, six, seven, or even more: some saw nothing but ribs in the branchial arches and jaws; others took the latter for limbs of the head, analogous to arms and legs. If they could not agree about the number of the vertebræ, still less were they at one in regard to the part assigned to each bone. The most bizarre nomenclatures have been proposed by different authors who thus sought to generalize their ideas. Some have gone so far as to pretend that the vertebræ of the head were as complete as the vertebræ of the trunk, and by means of dismemberments, with divers separations and combinations they have reduced all the forms of skull to vertebræ, assuming that the number of pieces was invariable for every form of skull, and that all vertebrate animals, whatever their definitive organization, bore, in their respective crania, the same number of points of ossification *."

And thus it is that a great truth in nature has been endeavoured, and

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* "C'est M. Oken qui fit imprimer le premier programme sur la signification des os du crâne. La nouvelle doctrine qu'il exposait fut accueillie en Allemagne avec un enthousiasme extrême par l'école des philosophes de la nature. L'auteur postulait alors trois vertèbres du crâne, et l'occipital basilaire, le sphénoïde et l'ethmoïde étaient envisagés comme les parties centrales de ces vertèbres craniennes. Sur ces prétendus corps de vertèbres s'élevaient des arcs enveloppant les parties centrales du système nerveux (nos plaques protectrices); tandis que du côté opposé étaient attachées des pièces inférieures qui devaient former l'arc végétatif destiné à embrasser le canal intestinal et les gros vaisseaux (les arcs de la face dont nous traiterons plus tard). Il serait trop long d'énumerer ici les changements que chaque auteur apporta à ce travail en le modifiant à sa manière. Les uns se contentèrent du nombre admis par Oken, les autres élevèrent le nombre des vertèbres craniennes jusqu'à quatre, six, sept et même plus; les uns voulurent voir des côtes dans les arcs branchiaux et les mâchoires; les autres prirent ces dernières pour des membres de la tête, analogues aux bras et aux jambes. Si l'on n'était pas d'accord sur le nombre des vertèbres on l'était encore moins sur le rôle qu'on assignait à chaque os. Les nomenclatures les plus bizarres ont été proposées par les différens auteurs, qui cherchaient ainsi à généraliser leurs idées. On alla jusqu'à prétendre que les vertèbres de la tête étaient aussi complètes que les vertèbres du tronc, et au moyen de démembremens, de séparations et de combinaisons diverses, on ramena toutes les formes du crâne à des vertèbres, en admettant que le nombre des pièces était invariablement fixé pour toutes les têtes; et que tous les vertébrés, quelle que soit d'ailleurs leur organisation définitive, portaient dans leur tête le même nombre de points d'ossification."—Recherches sur les Poissons Fossiles, t. i. (1843), p. 125.

too successfully in regard to the rising generation of anatomists, to be obscured. Ideas and statements are misquoted, unintentionally, doubtless, and through neglect of reference to the original work (as in the citation of the bones representing the bodies of the cranial vertebræ in the Okenian theory); or they are misunderstood (as where the arches, neurapophyses or 'bogentheile,' composed as Oken truly said by the alisphenoids and orbitosphenoids are held to be synonymous with the 'plaques protectrices' of M. Vogt): the most extreme and least defensible views are selected out of each tentative step in the inquiry, and are clubbed together to represent the general result, which is of course dismissed with as sweeping a condemnation. The specific objections raised by Cuvier are deemed well-founded and unassailable; and to these M. Agassiz adds the following. Assuming that, "the formation of vertebræ presupposes as a first condition the existence of a notochord*;" and, arguing upon this basis, and with a belief that the cephalic extension of the 'chorda dorsalis' as it is permanently manifested in the *Branchiostoma* is not so great in the embryos of other and higher fishes, but is arrested at the region of the alisphenoid from the commencement of its development, M. Agassiz concludes:—"Now, the application of this principle to the composition of the skull demonstrates at once that there exists *but one cranial vertebra, the occipital vertebra*, and that the rest of the skull is foreign to the vertebral system†."

At the period of development described and figured by M. Vogt in the embryo of the *Coregonus*, which period M. Agassiz conceives to represent the very earliest condition of the anterior extremity of the notochord, the pointed extremity of the gelatinous central cells of this part terminates at the posterior boundary of the hypophysial space: but the peripheral capsule of the notochord extends over that space and forwards to the obtuse anterior extremity of the embryonal 'basis cranii': and it is in the expanded aponeurosis, directly continued from the chorda along the basis cranii, that the thin stratum of cartilage cells are developed, arching along the sides of the hypophysial space, from which the ossification of the basisphenoid, presphenoid and vomer proceeds‡.

The superaddition or the later continuation of the cylindrical gelatinous 'chorda' in the aponeurotic basis of the cartilaginous and osseous growths of the vertebral centres in the trunk, seems to relate chiefly to their more or less cylindrical form in that region: the notochord regulates, as a mould, the course of ossification, disappearing by absorption as the bony lamellæ of the vertebral bodies encroach upon it in their centripetal progress: the notochord plays an important part also in the establishment of the elastic jelly-filled capsular joints in the back-bone of fishes; and therefore it might well be dispensed with, or be early and rapidly removed, in the development of the flattened, expanded and anchylosed or immoveably articulated bodies of the cranial vertebræ. And, besides, the notochord is immediately concerned in the development of only one of the elements of the typical segment of the endoskeleton. It is obviously, therefore, an unwarrantable and erroneous application of a developmental character, to conclude, from a modification of this one character in respect of a single element, the 'centrum,' that every other character establishing the general homology of such element, as

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* "La formation des vertèbres suppose, comme première condition, l'existence d'une 'corde dorsale.'"—*Op. cit.* tom. i. p. 127, livr. xviii. (1843.)

† "Or, l'application de ce principe à la composition de la tête nous montre d'entrée qu'il n'existe *qu'une seule vertèbre crânienne, la vertèbre occipitale*, et que le reste de la tête est étranger au système vertébrale."—*Ib.* p. 127.

‡ Hunterian Lectures on Vertebrata, 1846, p. 71.

well as every character determining that of the surrounding vertebral elements, are to be nullified and set aside! M. Agassiz, moreover, seems not to have suspected that the notochord may have other and more immediate and important functions than even those relating to the vertebral column. The peculiar elective attraction of its component cells for the gelatinous principle may be essential to the due operation of those neighbouring cells which form the basis of the neural axis, and which as exclusively assimilate the albuminous principle: and this reciprocal antagonism in the selection of particular proximate principles from the common primitive blastema may explain the contemporaneous origin of notochord and myelon in the embryonic trace, when all development is as yet the work of cell-assimilation and metamorphosis, without any supply from a vascular system, this being a later formation in the building up of the organic machinery. By confining, however, his views of the notochord to one of its functions in relation to a single vertebral element, and by extending his conclusions from this to the entire vertebra, M. Agassiz, though recognising more absolutely than Cuvier, the vertebral character of the neural arch of the occipital segment, concludes that Nature discards that type in the conformation of the bony cinctures that precede it and which successively girt the mesencephalon, prosencephalon and rhinencephalon.

Premising a gratuitous explanation of the hypothetical absence of the bodies of the cranial vertebræ (Poissons Fossiles, t. i. p. 128), M. Agassiz asks, "Ainsi, que seraient dans cette hypothèse, le sphénoide principal, les grandes ailes du sphénoide, et l'éthmoide, qui forment pourtant le plancher de la cavité cérébrale?—Des apophyses?—Mais, les apophyses ne protègent les centres nerveux que du côté et d'en haut?—Des corps des vertèbres?—Mais ils se sont formés sans le concours de la corde dorsale; ils ne peuvent donc pas être des corps des vertèbres." (*Ib.* p. 129.) To this it may be replied, first that the bodies of the cranial vertebræ are not absent; they are represented, as above explained, by their cortical portions in the vomer (fig. *5*, 13), presphenoid (*ib.* 9) and basisphenoid (*ib.* 5), and by both cortical and central portions in the basioccipital (*ib.* 1): nay, the central part of the body of the frontal vertebra is represented in some fishes by the entosphenoid (*ib.* 9'), which remains distinct from the cortical part below, as does the central part of the body of the atlas in the siluroid fish. If it were true, indeed, that the entosphenoid was pierced by the canals transmitting the olfactory nerves*, Bojanus' idea of its general homology as the centrum of the 'vertebra optica' must be abandoned. But the parts called 'olfactory nerves' by M. Agassiz, pass from the prosencephalic to the rhinencephalic compartments of the cranium not merely above the bone called 'cranial ethmoid' by the same author, but, also, through the upper part of the interspace between the bones (orbitosphenoids) which the entosphenoid (9') sustains: and the true olfactory nerves perforate the neurapophyses (14) which Bojanus called 'ethmoid' and which Cuvier and M. Agassiz have termed 'frontaux antérieurs' (see *ante*, pp. 46–58). The alisphenoids, being notched or perforated by their proper intervertebral nerves, are 'apophyses' (neurapophyses), and accordingly do protect the sides of their proper nervous centre, the mesencephalon. The central jelly-cells of the notochord appear to be withdrawn into the occipital region before ossification of the basisphenoid commences, and that modified vertebral body is therefore developed at the expense of the fibrous sheath of the notochord, and is represented by its 'cortical' part only. But its general homology is determined by its connections with the basioccipital (admitted by Agassiz to be a vertebral body) behind, and with the alisphenoids above.

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* M. Agassiz has described this bone under the name of 'éthmoide crânien' as "un os impair, court, de forme presque carré dans lequel sont percés les canaux servant aux nerfs olfactifs."—Recherches sur les Poissons Fossiles, t. i. p. 128.

In many fishes the basisphenoid unites with the basioccipital by a deeply indented sutural surface, like that which unites together the elongated bodies of the anterior trunk-vertebræ in the *Fistularia*. In mammals the basioccipital and basisphenoid join each other by flat surfaces, also like the bodies of the trunk-vertebræ, until the period when, in most of the class, the joint is obliterated by anchylosis. These and similar repetitions of class-characters of vertebral elements in the regions of the head and trunk are not so wholly devoid of signification, as they must seem to be to the opponents of the cranio-vertebral theory.

In his new and elaborate classification of the bones of the skull of fishes, M. Agassiz divides them primarily, like Cuvier, into bones of the *cranium*, or 'box which envelopes the brain and the organs of sense': and into bones of the *face*, 'which is composed of the moveable pieces subservient to nutrition and respiration' (*l. c.* p. 110).

This division is open to the objection that the bony or cartilaginous capsules which immediately envelope the organs of sense are always originally, and most of them permanently, separate from the box or capsule that envelopes the brain. The independent character of the ear-capsules, for example, is manifest on their first appearance in the ammocete; and, although they subsequently lose their distinctive features by the accumulation of cartilage-cells around them in which the foundations of the neurapophyses and parapophyses, contributing to the otocrane, are laid, one centre of ossification is commonly established, even in fishes, in special relation to the immediate protection of the vascular and nervous parts of the labyrinth.

As to the proper bony envelope of the eye, M. Agassiz does not enumerate it amongst the cranial bones of fishes: but admits into that series only the accessory protecting pieces which form the orbit; or rather only those that at the same time form the brain-case: for, the suborbitals, the entopterygoids and palatines are placed amongst the 'facial' bones: whilst the supraorbitals are transferred to another category of osseous pieces, the natural system here prevailing over the artificial one.

Subjoined* is an outline of the arrangement of the two primary classes of 'cranial' and 'facial' bones, founded upon the embryological researches of

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* CRANIAL BONES. (OS CRANIENS.)

A. EMBRYONIC BASIS (*'BASE EMBRYONALE,'* Vogt).

a. Nuchal plate (*'Plaque nuchale,'* V.). Basioccipital, Exoccipitals, Paroccipitals, Supraoccipital, Petrosals.

b. Lateral loops (*'Anses latérales,'* V.). Alisphenoids, Orbitosphenoids.

c. Facial plate (*'Plaque faciale,'* V.). Entosphenoid (l'ethmoïde crânien, Ag.).

B. PROTECTIVE PLATES (*'PLAQUES PROTECTRICES,'* V.).

a. Superior plates. Parietals, Frontals, Nasals.

b. Lateral plates. Prefrontals, Postfrontals, Mastoids (temporaux, Ag.).

c. Inferior plates (*'Plaque buccale,'* V.). Basi- pre- sphenoid, Vomer.

FACIAL BONES. (OS DE LA FACE.)

I. *Maxillary arch.* Suborbitals (jugaux, Ag.), Maxillary, Premaxillary.

II. *Palatine arch.* Palatines, Entopterygoids, Pterygoids (transverses, Ag.).

III. *Mandibular arch.* Pretympanics ('caisses,' Ag.), Mesotympanics ('tympano-malleaux,' Ag.), Hypotympanics ('os carrés,' Ag.), Mandible.

IV. *Hyoidean arch.* Epitympanics ('mastoïdiens,' Ag.), Preoperculars, Stylohyals, Epihyals, Ceratohyals, Basihyals ('l'os lingual,' Ag.).

V. VI. VII. VIII. *Branchial arches.* 'Composés chacun de deux ou trois pièces et reunis sous le gorge par le corps de l'hyoïde.'

IX. *Pharyngeal arch.* 'Composé d'une ou de plusieurs pièces,' &c.—*Op. cit.* t. i. pp. 124, 130.

M. Vogt. With regard to the series of nine arches into which the facial bones are distributed, it may be remarked that the independence of the maxillary from the palatine, which is more apparent than real in the osseous fishes, ceases to be manifested in any degree in the plagiostomes and lepidosiren: that the first and second arches are suspended by their crowns with their haunches projecting freely outwards, whilst the third and fourth arches are suspended, in the reverse position, viz. inverted, with the crowns or key-stones downwards: the four next arches are rather complete cinctures, their summits meeting and being loosely suspended to the basis cranii, or, in plagiostomes and cyclostomes, to the under part of the vertebral column of the trunk. Although professing to base his classification upon developmental characters, M. Agassiz owns with regard to the posterior branches of the maxillary arch, *e. g.* the suborbitals, "that they appear to be rather formed by the dermal system." And this is unquestionably true: whilst the palatines, which are the true piers of the arch, are developed from the blastema of the same visceral arch as the maxillaries and premaxillaries.

The error in regard to the special homology of the suborbital bones, determined by M. Agassiz as the malars, and which is so clearly exposed by the structure of the skull of the *Psittacidæ* (*ante*, p. 41), has misled him in respect to the natural and typical constitution of the maxillary arch.

The mistake in reference to the special homology of the epitympanic (28), determined by M. Agassiz as the 'mastoid,' has, in like manner, influenced him in dissociating it from the other dismemberments of the tympanic pedicle, and referring it to a different arch.

With regard to the hyoid and branchial arches, it will be observed that M. Agassiz makes no distinction between the systems of the neuro- and splanchno-skeleton. An arch constant and ossified in all vertebrates where the rest of the endoskeleton is ossified, and which, even admitting M. Agassiz' special homology of the preopercular as the styloid process of the temporal, would still be suspended in the inverted position, like a true hæmal arch, is placed in the same category as the branchial girdles, which are often cartilaginous when the hyoid is osseous, in bony fishes; and which disappear, in the metamorphosis of the tadpole, with the evanescent respiratory viscera for the support of which they are exclusively developed.

The constitution of a distinct 9th facial arch for the posterior pair of branchial girdles, which retain their gills in lepidosiren, though modified in subservience to mastication in most osseous fishes, appears to be giving undue importance to an artificial or adaptive character. Finally, the natural connections of the scapulo-coracoid arch in osseous fishes are totally disregarded, and it is left out of the enumeration of the bones of the head.

The unbiassed anatomist may find an element for judging of the natural character of the cranio-vertebral system propounded in the present Report, by contrasting the classification of the bones of the fish's skull to which it leads, with that proposed by M. Agassiz, and with nature*.

Having thus responded to the objections advanced by Cuvier and M. Agassiz to the interpretations of the segmental constitution of the bones of the head which were open to the criticism of those great authorities in anatomy, I proceed briefly to explain the segmental constitution of the bones

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* I am bound here to say that in the discussion of the subject of this Report with M. Agassiz, which, amongst other advantages of the meetings of the British Association, I enjoyed at Southampton, he admitted, with his characteristic frankness, that some points of his classification of the bones of the head in fishes would require reconsideration. One of the eminent physiologists who was present at the debate which followed the reading of the Report, has recorded the impression it produced upon him in a review of my 'Hunterian Lectures on Vertebrata' in 'The British and Foreign Medical Review,' No. xlvi. p. 496.

of the trunk of the human subject according to the archetypal vertebra with which the segments in the head have been illustrated.

The first seven segments of the trunk consist each of centrum (fig. 25, *c*), neurapophyses (*n*), neural spine (*s*), and rudimental pleurapophyses (*pl*), which coalesce, in each segment, into one bone, called 'cervical vertebra' in anthropotomy. If the hæmapophyses (*ss*') have the same relation to their centrum which those of the seventh dorsal vertebra, in the *Ciconia Argala*, more obviously bear to theirs,—that is, being attached below and disunited at their upper ends from their pleurapophyses, which are short, stunted and anchylosed to the centrum,—and if, as the apparent homologues of *ss*' in fishes would indicate, the atlas be actually the centrum to which such detached and shifted hæmapophyses belong, then the first will be the sole segment of the cervical region of the trunk in which those elements are ossified.

In the seven vertebræ which succeed the cervicals the pleurapophyses (*pl*) are progressively elongated; they are shifted from their proper centrum to the interspace between it and the next segment above, or in advance, and retain their moveable joints. The hæmapophyses (*h*) are cartilaginous and articulate with the ends of the pleurapophyses and with the hæmal spines (*hs*), which are flattened, slightly expanded, and ultimately blended into one bone called 'sternum.' The hæmal spine of the first typical segment remains longest distinct: it receives, also, the extremities of the displaced hæmapophyses (*ss*') and has been called 'manubrium sterni.' The hæmal spine of the seventh segment commonly continues longer distinct, and is later in becoming ossified, whence it is called 'ensiform cartilage': it probably includes the rudiments of some succeeding hæmal spines. In the four succeeding segments the pleurapophyses become progressively shorter, and the hæmapophyses, still cartilaginous, are severally attached by their lower attenuated ends to the pair in advance; leaving the hæmal arch incomplete below. In the next vertebra (19th from the skull) the still shorter pleurapophyses resume the exclusive articulation with their proper centrum; and the correspondingly short and pointed hæmapophyses terminate freely.

Those pleurapophyses and hæmapophyses which directly articulate with hæmal spines (sternum) are called collectively 'true ribs' (costæ veræ), the proximal element being 'the bony part of the rib' (pars ossea costæ), the distal one the 'cartilage of the rib.' The rest of the hæmal arches which are incomplete through the absence of the hæmal spine, are called 'false ribs' (costæ spuriæ); and the last, which terminates freely in the origin of the diaphragm, is a 'floating rib.' The centrum, neurapophyses and neural spine of each segment with freely articulated pleurapophyses coalesce into one bone, called 'dorsal vertebra' in anthropotomy: these vertebræ are twelve in number. Each of the five succeeding segments is represented by the same elements (centrum and neural arch) coalesced that constitute the so-called dorsal vertebræ: they are called 'lumbar vertebræ' (fig. 25, L.): they have no ossified pleurapophyses; and the hæmapophyses of these segments are represented only by the aponeurotic 'inscriptiones tendineæ musculi recti' (*h*").

Certain elements of the five succeeding segments (*ib.* S.) coalescing together in the progress of growth form the bone called 'sacrum': and are described individually as sacral vertebræ. The first four of these each combine the same elements, coalesced, as in the neck; viz. centrum, neurapophyses, neural spine, and short but thick pleurapophyses*: in the fifth sacral vertebra there are no

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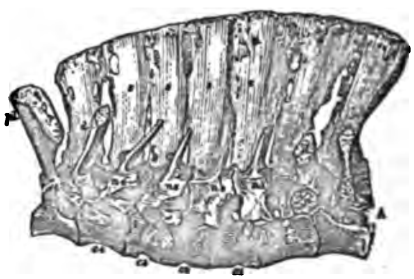
* J. Müller notices the rudimental ribs in the first and second sacral vertebræ of the human fœtus in his Anatomie der Myxinoiden, heft i. 1834, p. 240. Mr. Carlile has described (Report of British Association, 1837, p. 112), and Dr. Knox has figured (Lancet, 1839, p. 191) these ribs and their homotypes in the third and fourth sacral vertebræ.

osseous rudiments of pleurapophyses; and the neural spine is commonly undeveloped. One or more typical segments are obviously completed by the meeting of the broad sides of the inverted arch (62, 63, 64) at the 'ischio-pubic symphysis' forming the 'pelvis' of anthropotomy. Before, however, entering upon the difficult inquiry into the general homology of the pelvis, I would beg to refer the reader to the analysis of the sacrum of the ostrich given at p. 95: and I here subjoin a figure of seven of those vertebræ, from an immature specimen, the pleurapophyses being removed from all save the last (*pl*), in order to show the change of place of the neurapophyses *n* 1–4, in relation to their centrums, *c* 1 to 4: *d d* are the long diapophyses; *p* the short parapophyses. The sacral spines, *s s*, are enormously developed.

In the bird the modification of the vertebral segments at the posterior region of the trunk in relation to the transference of the whole weight of the body and fore-limbs (wings) upon the hind-limbs, is greater and more extensive than in the 'bipes implume,' and the essential nature of the pelvic arch is still more masked in the bird than in man. In order to obtain an insight into the model according to which it is constructed, we must descend still lower, even to the humblest of the vertebrated creatures that crawl upon the earth. The example which is here selected for that purpose is the perennibranchiate amphibian called *Menopome Alleghanniensis*.

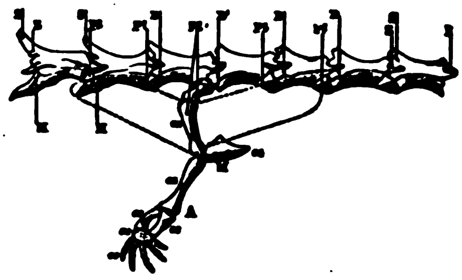
Fig. 27.



7 sacral vertebræ of a young ostrich (*Struthio camelus*).

The three anterior vertebræ which answer in position to the 'lumbar' in fig. 25, differ chiefly in having rudimental pleurapophyses (*Pl*) articulated to the ends of the diapophyses (*D*). In the next vertebra the diapophysis (*D'*) and the rudimental pleurapophysis (*Pl'*) are thickened and enlarged: a second pleurapophysial rib-like piece (62) is joined by one end to the pleurapophysis, and by the other to a broad partially ossified cartilage (64) which meets and joins its fellow, completing a hæmal arch and raising the vertebra in question to the typical character. A radiated appendage, moreover, diverges on each side from the articulation between 62 and 64, and forms the hind-limb. Now the special homology of this limb with the undivided filamentary appendage similarly situated in the lepidosiren, and with the ventral fins of fishes, in the descending series; and with the hind-limb of other reptiles, of birds and of mammals in the ascending series, is unmistakeable, and, I believe, is generally admitted: so that comparative anatomists have not hesitated to call the rib-like bone, 62, 'ilium,' and the part, 64, 'pubis' in the menopome.

Fig. 28.



Sacral vertebra and appendage with contiguous vertebræ. Menopome.

The special homologies of these elements of the pelvis being thus determined, it follows, that their general homology, as it may be revealed by the simple condition of the pelvic arch in the species in which the pelvis, as complete and fixed to a sacrum, makes its first appearance in the animal kingdom, will be equally applicable to the parts under all their metamorphoses in the higher air-breathing vertebrates.

The correspondence of the segment of the endoskeleton in the menopome D′, Pl′, H, A, with the typical vertebra, as illustrated by fig. 15, is such, that any other explanation of its essential nature than as a representative or repetition of such fully developed segment or vertebra seems contrary to nature. The chief modification has its seat in the most peripheral part or appendage A, as compared with its simple homologue in the thoracic segment of the bird (fig. 15). If 62 and 64 are to be regarded as strangers to the vertebral system, new parts introduced for special purposes, and not as normal elements modified for such purposes, I am at a loss to know on what principles, or by what series of comparisons we can ever hope to attain to the higher generalizations of anatomy, or discover the pattern according to which the vertebrate forms have been constructed. It may be said that the arch which they constitute performs a new function, inasmuch as it sustains a locomotive limb which reacts upon the ground. But this new function arises in the menopome, rather out of the modifications of the appendage than of the arch itself. In so far as the mere support of the appendage is concerned, the inverted or hæmal arch Pl′, H, performs no new function, but one which is common to such arches in the thorax of birds, and to the less completely ossified homologous arches in the abdomen of fishes, where moreover the simple diverging appendages do give attachment to the muscles of locomotion. Comparing, then, the hæmal arch in question with that of the typical vertebra (fig. 15), we find that, like the scapulo-coracoid arch in fishes (fig. 5, H 1), its parts are open to two interpretations. The upper piece of *Pl′* may be the whole pleurapophysis, the lower, 62, the hæmapophysis, and the part, 64, the half of an expanded and bifid hæmal spine: or *Pl′* with 62, may be two portions of a teleologically compound pleurapophysis, and 64 the hæmapophysis, which would join with its fellow without, or with a mere rudiment of, a hæmal spine intervening. From the analogy of the scapulo-coracoid arch in fishes, which is proved by its modifications in higher animals to want the hæmal spine, it is most probable that such is the condition and true interpretation of the correspondingly simple pelvic arch under consideration. But the general relation of this arch to the hæmal one of the typical segment is not affected by the alternative.

I regard, therefore, *Pl′*, 62, as two portions of a fully developed pleurapophysis; and the pleurapophyses, *Pl*, *Pl* of the contiguous vertebræ as answering only to the upper portion of the pelvic one. In ascending from the menopome to the crocodile, we find the homologue of 62 broader than it is long, and articulated to the thickened proximal portions of the pleurapophyses of two segments; and we observe, likewise, the pelvic arch completed below by two pairs of hæmapophyses: for the anterior pair the name of 'ossa pubis' is retained; to the posterior pair that of 'ischia' is given. In general homology these bones complete, as hæmapophyses, the two vertebral segments modified to form the sacrum of the crocodile; and the intermediate connecting piece (ilium) may be interpreted, as either the confluent distal portions of the pleurapophyses of both vertebræ, or as an expansion of one such portion, answering to 62 in the menopome, and intruding itself between the stunted pleurapophysis and distant hæmapophysis of the second sacral vertebræ in the crocodile.

In the bird the expansion of the element 62 proceeds to a further extent, and besides the proximal piece of the pleurapophysis of its own segment, the bone 62 is brought into connection with the homologous stunted or proximal ends of pleurapophyses of several contiguous segments, in the manner indicated by the dotted line in fig. 28, and in Pl. II. fig. 4, 62. Now, if the ilium, so expanded, were interpreted as the coalesced complementary portions of all the short pleurapophyses with which it articulates, its condition would be very similar to that which Oken has attributed to the scapula. But its ossification radiates, as in the simple rib-like ilium of the menopome, from a common centre: there are no corresponding multiplications of hæmapophyses below; these are restricted in the pelvis of all animals to the number which they present in the crocodile. And since the scapula has been proved to be, under its most expanded form, the homologue of a single pleurapophysis, so also I am disposed to regard its homotype, the ilium, as maintaining under every variety of form and proportion, the same fundamental singleness of character, as it presents on its first appearance in the perennibranchiate batrachian.

The first sacral vertebra, then, in man is complete; but its pleurapophysis is divided, and the lower portion expanded to form the so-called 'ilium' (62). The hæmapophysis (64) coalesces with that of the succeeding vertebra (63), and with its own pleurapophysis (62, fig. 25, and Pl. II. fig. 6).

The second sacral vertebra has its hæmapophysis (63, called 'ischium') ossified, but separated from its proper pleurapophysis by the expanded (iliac) portion of that of the preceding vertebra, with which it coalesces, as well as with the preceding hæmapophysis (pubis). The short and thick pleurapophyses of the third sacral vertebra also articulate in the adult with the expanded distal portions of those of the first sacral vertebra: but these (iliac bones) are restricted in infancy and early childhood to their connections with the first and second sacral vertebræ, which connections are permanent in most reptiles (Pl. II. fig. 3).

The fourth sacral vertebra consists, in man, of centrum, neurapophyses, and rudimental pleurapophyses; the fifth sacral vertebra of centrum and rudimental neurapophyses, which rarely meet above the neural canal.

In each sacral vertebra the elements of the neural arch and rudimental ribs first coalesce together; and afterwards the vertebræ unite with each other and form the anthropotomical bone called 'sacrum.'

The first coccygeal vertebra in man consists of a centrum and of stunted neurapophyses* wide apart above, but developing zygapophyses, which join those of the last sacral vertebra, and diapophyses which extend outwards further than those of the same vertebra. The neurapophyses are represented by exogenous tubercles of bone in the second coccygeal vertebra; and the third and fourth vertebræ are reduced to the centrums only.

The cartilaginous deposits in the primitive blastema of this extremity of the trunk indicate a greater number of caudal vertebræ, and the rudimental tail is proportionally longer in the embryo than in the adult. It is shortened, however, by absorption prior to the commencement of ossification, and but four segments are indicated by depositions of the earthy salts in the situations proper to the above-specified elements of a typical vertebra: these finally coalesce into a single bone "of a crooked pyramidal figure," which got its name of 'os coccygis' from its supposed resemblance to a cuckoo's beak †.

The early recognition of these and other specialities arising out of the various adaptive modifications of the typical segments of the human skeleton found its expression, necessarily, in special terms, the convenience of which will ensure their permanence; but the progress of anatomical science having unfolded the primary form which is the basis of those modifications, there arises the same necessity for giving utterance to ideas of the generic character of the parts by general terms.

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* "Shoulders of the os coccygis."—Monro, l. c. p. 142. † Ib. p. 141.

Inasmuch, however, as the different segments of the human skeleton deviate in various degrees from the common archetype, and as the different elements of such segments differ in their modifiability, anthropotomy has at no period wanted also its 'general terms' expressive of the recognised extent of such conformity: such terms also, indicating, obscurely indeed, so much perception of the pre-existing model as could be obtained from the study of one form, at a period when that form—the human frame—was viewed as something not only above, but distinct from, if not antithetical to the structures of the brute creation, and when it was little suspected that all the parts and organs of man had been sketched out, in anticipation, so to speak, in the inferior animals. Thus the word 'vertebra' shows, by the number of the segments or parts of segments to which it is applied in anthropotomy, a recognition of the degree in which the principle of repetition of similar parts more obviously prevails in the construction of the human endoskeleton. And, inasmuch as in some regions (the cervical, *e.g.*) the 'vertebra' includes all the elements of the typical segment, there developed, it has been retained in homological anatomy, but, with a more consistent and definite meaning, as the technical term of the primary segment of the endoskeleton in all vertebrate animals.

The 'true vertebræ' of anthropotomy are those segments which retain the power of moving upon each other; and the term is applied in a peculiar and empirical sense very different from the meaning which the anatomist attaches to a true or typical vertebra. The 'false vertebræ' of anthropotomy are those segments or parts of segments forming the lower or hinder extreme of the endoskeleton, and which do not admit of reciprocal motion at their joints. And Monro, admitting that the condition of even the human os coccygis sometimes militates against the definition, meets the objection by arguing for the speciality of that bone, and with as good or better reason than those who have subsequently contended against admitting the cranial segments into the category of vertebræ. "From the description of this bone" (os coccygis), "we see how little it resembles *vertebræ*; since it seldom has processes, never has any cavity for the spinal marrow, nor holes for the passage of nerves*."

Embryology has since demonstrated that the parts of the os coccygis are originally in vertebral relation with the neural axis; and that this is subsequently withdrawn by a concentrative movement, which in like manner withdraws it from the terminal segment at the opposite extreme of the endoskeleton. The homology of the divisions of the sacrum with the true vertebræ is admitted by Monro, because of the perforations for the nerves: and this character is still retained in the nasal vertebra in the form of the cribriform foramina, although its neurapophyses, like those of the sacrum, have lost their primitive relation to the neural axis.

Homological anatomy, therefore, teaches, that the term 'vertebra' should not only be applied to the segments of the human skeleton in the technical and definite sense illustrated by figs. 14 and 15, but be extended to those modified and reciprocally immoveable segments which terminate the endoskeleton superiorly, and are called collectively 'skull.' (Pl. II. figs. 1 to 6, Cr.)

The term 'head,' then, indicates a region of specially modified vertebræ, like the terms 'neck,' 'chest,' 'loins,' &c.; and amongst the species of the primary segments characterized by specific modifications, the 'cranial' vertebræ must be added to the 'cervical,' 'thoracic or dorsal,' 'lumbar,' 'sacral,' and 'coccygeal or caudal.'

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* Monro, *l. c.* p. 143.

Such, with reference to the 'general' term 'vertebra,' seems to be the advance of which anthropotomical science is susceptible, in order to keep progress and be in harmony with anatomy.

As to the elements of the typical vertebra, anthropotomy has also its general phrases (see Table II. column vi. 'Soemmerring.'), some of which are equivalent to the clearly defined technical terms of such elements in anatomy properly so called.

The serial homology of the centrum (*corpus vertebræ*) has been recognised in all the so-called 'true vertebræ,' and in some of the 'false vertebræ:' thus Monro says, "The fore-part of the *os sacrum*, analogous to the bodies of the true vertebræ, is smooth and flat[*]." But their smooth and flat homotypes in the skull have only the special names of 'basilar' and 'cuneiform' processes; of 'processus azygos' and 'vomer.' The 'neurapophyses' are recognised as repetitions of the same part under the definitions of 'a bony bridge produced backwards from each side of the body of the vertebra,' of '*arcus posterior vertebræ*,' of 'vertebral laminæ' or 'pedicles.' Monro describes these rudimental elements in the last sacral vertebra as 'knobs,' and in the first coccygeal vertebra as its 'shoulders.' In the skull they receive the special definitions of "the pieces of the occipital bone situated on each side of the great foramen; from which nearly the whole condyles are produced[†]" (*partes laterales seu condyloideæ*, Soem.); 'great' or 'temporal wings of the sphenoidal bone[‡];' 'orbitar wings' or 'processes of the sphenoidal bone;' 'nasal' or 'vertical plate' and 'crista galli' of the ethmoid ('*pars media ossis ethmoidei*,' Soem.).

The neural spines are called generally '*spinal processes*' in every segment of the trunk: in the head they are known only by the special names of 'occipital plate,' 'parietal bones,' 'frontal bone,' 'nasal bones.'

The pleurapophyses, when free, long, and slender, are called '*ribs*,' 'vertebral ribs,' or 'bony parts of the ribs'; when short and anchylosed, they are called, in the neck, "the second transverse processes that come out from the sides of the body of each vertebra[§];" (*radix prior processus transversi vertebræ*, Soem.;) in the sacrum 'transverse processes' and 'ilium'; in the skull, 'scapula', 'styloid process of the temporal bone,' 'external auditory or tympanic process of the same bone'; 'palatine bone.'

In like manner the serial homology of the hæmapophyses is recognised in the thoracic region by the general term 'cartilages of the ribs' or 'cartilages of the sternum'[‖] there applied to the same elements of twelve successive segments. When ossified in other vertebræ they have received the special names of 'ischium,' 'pubis,' 'coracoid process of the scapula,' 'clavicle,' 'appendix or lesser cornua of the hyoid bone,' ('*crura superiora*,' '*os linguale superius*,' Soem.), 'lower jaw' or *mandibula*, 'upper jaw' or *maxilla*.

The exigences of descriptive anthropotomy and its highly important applications to Medicine and Surgery necessitate such special nomenclature, and the reform which that nomenclature chiefly requires is the substitution of names in the place of phrases for the parts of the human body.

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[*] Monro, *l. c.* p. 138. [†] *L. c.* p. 76. [‡] *L. c.* p. 86. [§] *L. c.* p. 126.

[‖] Laurentius, in describing the human thoracic pleurapophyses, says, "Earum duplex est articulatio, altera cum spondylis dorsi, altera cum sterni cartilaginibus" (Anatomica Humani Corporis, Fol. 1600, p. 94). The perception of the essential distinctness of the vertebral ribs had not then been blunted by the constant repetition of the conventional idea of their forming an ossified part of a whole, completed by the hæmapophysis under the name of the 'cartilago costæ.' In birds it is not uncommon to find the hæmapophyses not only ossified, but some of them attached to the sternum, and detached from the pleurapophyses.

But the retention and use of specific names for specially modified elements in the different segments by no means preclude the entertainment of general ideas and the necessity of expressing them by generic names for the homologous elements in the entire series of vertebræ.

If anthropotomy is to make corresponding progress with anatomy, and to derive the same light from the generalizations of zootomical science which medical botany has done from general botanical science, its nomenclature must expand to receive those generic terms which express the essential nature of the parts, heretofore named and known only according to the results of particular and insulated observation. A term which truly expresses the general homology of a part enunciates the most important and constant characters of such part throughout the whole animal series, and implies therefore a knowledge of such characters in that part of the human body, when used and understood by the human anatomist. Before the cuneiform process of the occipital bone could be defined as the 'occipital centrum,' the modifications and relations of the homologous part in all classes of vertebrate animals had to be accurately determined. The generic homological term expresses the sum or result of such comparisons, and the use of such terms by the anthropotomist implies his knowledge of the plan or pattern of the human frame which lies at the bottom of all the modifications that raise it to an eminence so far above those of all other vertebrate animals.

In no species, however, is each individual segment of the endoskeleton so plainly impressed with its own individual characters, as in Man; the practised anthropotomist, for example, will at once select and name any given vertebra from either the cervical, the dorsal, or the lumbar series. During that brilliant period of human anatomy which was illuminated by a Fabricius, an Eustachius, a Fallopius, and a Laurentius, the terms expressive of the recognition of such specific characters were more numerous and often more precise than in our modern compilations. Pleurapophyses were individualized in the thorax as well as in the head: the 'antistrophoi,' 'stereai' and 'sternitides,' for example, were distinguished from the other 'pleural gnesiai'*.

General anatomical science reveals the unity which pervades the diversity, and demonstrates the whole skeleton of man to be the harmonized sum of a series of essentially similar segments, although each segment differs from the other, and all vary from their archetype.

CHAPTER III.—SERIAL HOMOLOGY.

Since, then, we are led by the observations, comparisons and reasonings recorded in the preceding parts of this Work, to recognise, as the fundamental type of the vertebrate endoskeleton, a series of segments repeating each other in their essential characters, it follows that, not only the power of determining the homologous bones throughout the vertebrate series, but also throughout the vertebral segments of the same individual, is included in such generalization.

The recognition of the same elements throughout the series of segments of the same skeleton I call 'the determination of serial homologies.' This kind of study appears to have been commenced by the gifted Vicq d'Azyr, in his 'Mémoire' entitled "Parallèle des os qui composent les extrémités," printed in the Mémoires de l'Académie des Sciences for the year 1774, and

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* Anatomica Humani Corporis, &c., multis controversiis et observationibus novis illustrata. Andr. Laurentio, fol. 1600, p. 95.

Condorcet, in his Report on this ingenious Essay, speaks of it as "un essai d'une autre espèce d'Anatomie comparée, qui jusqu'ici a été peu cultivée."

Vicq d'Azyr compares, or points out the serial homology of, the scapula with the ilium, the humerus with the femur, the two bones of the fore-arm with the two bones of the leg, the small bones of the carpus with those of the tarsus, the metacarpus with the metatarsus, and the fingers with the toes. He is not so happy in his particular as in his general determinations: his choice in the leg, for example, of the homotypes of the radius and ulna in the fore-arm, is erroneous; but the whole memoir is an admirable example of the appreciation of correspondences which later researches in the same direction have proved to flow from a higher and more general law of uniformity of type. It is, indeed, a striking instance of the secret but all-prevailing harmony of the vertebrate structure that serial homologies should be determinable to such an extent in the parts of the diverging appendages, which are the seat of the greatest amount and variety of deviations from the fundamental type.

It will, of course, be obvious that the humerus is not 'the same bone' as the femur of the same individual in the same sense in which the humerus of one individual or species is said to be 'the same bone' as the humerus of another individual or species. In the instance of serial homology above-cited, the femur, though repeating in its segment the humerus in the more advanced segment, is not its namesake, not properly, therefore, its 'homologue'. I propose, therefore, to call the bones so related serially in the same skeleton 'homotypes,' and to restrict the term 'homologue' to the corresponding bones in different species, which bones bear, or ought to bear, the same names.

In the skull those bones are homotypes, or repetitions of the same essential part in the series of vertebral segments, which succeed each other lengthwise, as in the last four columns of the subjoined Table:—

VERTEBRÆ.	OCCIPITAL.	PARIETAL.	FRONTAL.	NASAL.
Centrums	Basioccipital	Basisphenoid	Presphenoid	Vomer.
Neurapophyses	Exoccipital	Alisphenoid	Orbitosphenoid ..	Prefrontal.
Neural spines	Supraoccipital ..	Parietal	Frontal	Nasal.
Parapophyses	Paroccipital	Mastoid	Postfrontal	None.
Pleurapophyses	Scapula	Stylohyal	Tympanic	Palatal.
Hæmapophyses	Coracoid	Ceratohyal	Articular	Maxillary.
Hæmal spines	Episternum	Basihyal	Dentary	Premaxillary.
Diverging appendages ..	Fore-limb or fin	Branchiostegals ..	Operculum	Pterygoid and Zygoma.

Thus the basioccipital, basisphenoid, presphenoid and vomer are homotypes with the centrums of all the succeeding vertebræ. The exoccipitals, alisphenoids, orbitosphenoids, and prefrontals, are homotypes with the neurapophyses of all the succeeding vertebræ. The paroccipitals, mastoids and postfrontals are homotypes with the transverse processes of all the succeeding vertebræ. The supraoccipital, parietal, frontal and nasal are homotypes with the vertebral neural spines.

The petrosals, sclerotals, and turbinals are homotypes of each other, as being respectively sense-capsules of the splanchno-skeleton.

The suprascapula and scapula are together the homotypes of the stylohyal and epihyal; of the tympanic, whether single or divided; and of the palatal: and all these are the homotypes of the pleurapophyses collectively, whether modified as ribs, hatchet-bones, or iliac bones, in the rest of the vertebral segments.

The coracoid is the homotype of the ceratohyal, this of the articular division of the mandible (with its subdivisions called angular, sur-angular and coronoid, in cold-blooded animals), and this, again, of the maxillary bone: all four being homotypes of the hæmapophyses of the remaining vertebral segments, whether modified to form clavicles, pubic bones or ischia, chevron-bones, sternal ribs, abdominal ribs, cartilages of ribs, abdominal cartilages or tendinous intersections of the modified intercostal muscles called 'recti abdominis.'

The entosternal, when present, is the homotype of the basihyal, of the dentary or premandibular, and of the premaxillary bones; and these collectively are homotypes of the hæmal spines of the rest of the vertebral segments, whether retaining their spinal shape as in the caudal hæmapophyses, or flattened as ordinary 'sternal bones,' or expanded and subdivided, like the neural spines in the cranium, in order to complete below the thorax of the bird or to form the plastron of the turtle[*].

There reigns a beautiful parallelism in the kind and degree of modification of the parts of the neural with the corresponding parts of the hæmal arch of the same vertebral segment: and as the serial homologies which have just been enunciated succeed each other longitudinally (horizontally in beasts, vertically in man) in the axis of the vertebral column, so these manifest themselves in a direction perpendicular to that axis.

The manubrium sterni of the bat developes a spine downwards, as the supraoccipital of the fish sends a spine upwards: the expanded manubrium sterni of the whale repeats the condition of the supraoccipital in birds and mammals. The form of the ordinary sternal bones in mammals is repeated by the parietal and supraoccipital bones of the crocodile. The divided sternum of the young ostrich, before the two lateral ossifications have coalesced at the median suture, repeats the condition of the divided parietal in most mammals. The development of the crista from the obliterated suture of the lateral halves of the expanded hæmal spine in the thorax of birds is paralleled by the development of the crista from the obliterated suture of the expanded neural spine in the cranium of carnivores. The interposition of the entosternal piece in the chelonian carapace parallels below the interposition of the interparietal bone in the rodent cranium above.

Thus modifications and developments of the same kind and degree manifest themselves in the upper (neural) as in the lower (hæmal) peripheral elements of the vertebræ; and though not always in the same vertebra, nor in the same animal, yet they are sufficiently exemplified in the myelencephalous series generally, to establish the conclusion that the hæmal spines under all their modifications are vertical homotypes, not of the centrums, as Oken, Meckel and De Blainville have supposed, but of the neural spines of the same vertebræ. In the composition of the neural arch of the occipital, parietal and frontal vertebræ, we find the neurapophyses repeating the pleurapophyses of the hæmal arch, and the parapophyses repeating the hæmapophyses in their relative positions to the centrum and the spine or key-bone of such arches.

Symmetry, polarity, or serial homology of parts of the same vertebral segment is usually still more strictly preserved in the transverse direction, and is so obvious, as to have immediately led to the detection of the homologous parts, which are accordingly distinguished as 'right' and 'left.'

Returning to the consideration of those serial homologies with which Vicq d'Azyr commenced the study of these relations, I may remark that the bones of the fore- and hind-limbs of some of the marsupial quadrupeds best illustrate the true relations which my revered Preceptor in Anatomy, Dr. Barclay[†], was, I believe, tha first to enunciate in respect of the bones of the fore-arm and leg.

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[*] These homotypical relations will be readily traced by the markings characteristic of the vertebral elements in Plate II.

[†] In his explanations of Mitchel's Plates of the Bones, 4to, 1824, pl. 24, figs. 3 and 4, Dr. Barclay, without referring to Vicq d'Azyr's Memoir, simply enunciates the correct view of the serial homology of the bones of the fore-arm and leg, as follows:—"On com-

The skeleton of the *Phalangista* or *Phascolomys* plainly demonstrates that the tibia (Pl. II. fig. 16, *66*) is the homotype of the radius (*ib.* fig. 15, *55*, and that the fibula (*ib.* fig. 16, *67*) is the homotype of the ulna (*ib.* fig. 15, *54*). In the wombat the part of the fibula (*67′*) representing the olecranon (*o*) is a detached sesamoid, as the olecranon itself is in the penguin and the bat: in the ornithorhynchus the fibula assumes those proportions and developes that process from its proximal end, the want of which in man and most mammals deceived Vicq d'Azyr, as it has misled, more recently, M. Cruvelhier. The complex explanation of the serial homologies of the bones of the upper and lower extremities proposed by the last named pains-taking anthropotomist*, involves more unnatural transpositions and combinations of the parts than those of the D'Azyrian hypothesis, which its ingenious author could not but admit seemed paradoxical; viz. that the anterior member of one side of the body repeated or corresponded with the posterior member of the opposite side. Cuvier, however, seems to sanction this idea by repeating the statement of Vicq d'Azyr, "C'est la droite d'une paire, qu'il faut comparer à la gauche de l'autre†."

M. Flourens has exposed in detail the fallacies of this view in an excellent memoir in the 'Annales des Sciences' for 1838 (t. x. p. 35); in which he arrives at the same conclusions as Dr. Barclay, and from similar considerations from Comparative Anatomy, as to the serial homologies of the bones of the fore-arm and leg; and he confirms those of the carpal and tarsal bones, which had been so truly and acutely discerned by Vicq d'Azyr.

In mammalian quadrupeds generally the fore-limb takes the greater share in the support, the hind-limb in the propulsion of the body. The *manus* is accordingly commonly shorter and broader than the *pes*; this may be seen in the terminal segment of even the monodactyle hand and foot of the horse. Consequently the transverse direction prevails in the arrangement of the carpal bones and the longitudinal in that of the tarsal bones. The difference is least in the carpus and tarsus of the long and slender fore- and hind-hands of the quadrumana. If the carpus of the chimpanzee, for example, be compared with that of man, the first difference which presents itself is the comparatively small proportion of the scaphoid which articulates with the radius, as compared with that in man, in whom the distal articulation of the radius is equally divided between the scaphoides and lunare which are on the same parallel transverse series. In the orang (Pl. II. fig. 13), the divided scaphoid (*s*, *s′*) extends, almost as much from the os lunare as from the radius, along the radial side of the carpus, to reach the trapezium (*t*) and trapezoides (*z*); it is in great part interposed between the lunare (*l*) of the proximal row and the trapezium and trapezoid of the distal row of the carpal bones. The similarity of its connections, therefore, in the carpus with those of the scaphoid in the tarsus (Pl. II. fig. 14, *s*) is so close that the serial homology of the two bones is unmistakeable. The

paring the atlantal (pectoral) and sacral (pelvic) extremities, the fibula is found to be the bone corresponding to the ulna; and accordingly, upon extending our researches to Comparative Anatomy, we perceive it exhibiting the like variety and unsteadiness of character, sometimes large, sometimes small, and sometimes merely a process of the tibia," &c. He does not push his comparison to the bones of the distal segment of the limbs.

* "L'extrémité supérieure du tibia est représentée par la moitié supérieure du cubitus, et la moitié inférieure du tibia par la moitié inférieure du radius; tandis que le péroné est représenté par la moitié supérieure du radius et par la moitié inférieure du cubitus."—*Anatomie Descriptive*, t. i. p. 315.

† Leçons d'Anat. Comp. t. i. 1836, p. 342.

astragalus (*ib.* *a*), then, in the foot, repeats the os lunare (*l*) in the hand, but usurps the whole of the articular surface of the tibia, and presents a larger proportional size, especially in man, whose erect position required such exaggerated development of the astragalus, or homotype of the lunare. The prominent part of the calcaneum (Pl. II. figs. 6 and 24, *cl'*) obviously repeats the prominent pisiforme (fig. 6 and 13, *p*), and the body of the calcaneum (fig. 6 and 14, *cl*) articulates with the fibula, as the cuneiforme (fig. 6 and 13, *cu*) articulates with the ulna. The strain upon the homotype of the pisiforme (*cl'*) to produce the required effect in raising the back-part of the foot with its superincumbent weight upon the resisting ends of the toes, required its firm coalescence with the homotype of the cuneiforme; in other words, the cuneiforme and pisiforme of the carpus represent together the os calcis of the tarsus. With regard to the other bones there is no difficulty; the cuboid (fig. 14, *b*) supports the two ulnar digits, *iv*, *v*, of the foot, as the unciform bone (*u*) does those, IV, V, of the hand: the ecto-cuneiform (fig. 14, *ce*) supports the digitus medius, *iii*, of the foot as the os magnum (*m*) does that of the hand: the meso-cuneiform (fig. 14, *cm*) supporting the toe, *ii*, is the homotype of the trapezoid supporting the finger, II, and the ento-cuneiform (fig. 14, *ci*) is the homotype of the trapezium (fig. 13, *t*).

It is no unusual exception that of two essentially distinct bones in one segment being represented by their coalesced homotypes—a single bone—in another segment, as in the explanation above given of the serial homology of the calcaneum. The scaphoides and astragalus in the tarsus of the cat and wombat (fig. 16, *sc*, *a*) are represented by the single scapho-lunar bone in the carpus (fig. 15, *sc*, *l*). The scaphoid and a cuneiform bone in the tarsus of the sloth and megatherium are represented by the single scapho-trapezium in the carpus. The scaphoid and unciform bones in the carpus of the ox are represented by the single 'scapho-cuboid' bone in the tarsus (fig. 18, *s*, *b*).

I have long entertained the opinion that an appreciation, vague and indistinct, perhaps, of certain serial homologies, may have been associated with, if it did not suggest, the epithets "scapula of the head," "femur of the head," &c. applied to certain cranial bones by Oken and Spix.

To Cuvier this language seemed little better than unintelligible and mystical jargon, and he alludes to it with ill-disguised contempt[*]. It has been commonly cited by those who have followed the great palæontologist in depreciating the cranio-vertebral theory, as a sufficient instance, needing no comment, of the extravagances essentially inherent in such attempts to recognise and explain the fundamental pattern to which the modifications of the cranial bones are subordinated. And it must be confessed that the expressions by which the philosophical anatomists of the school of Schelling have endeavoured to illustrate in the animal structures the transcendental idea of 'the repetition of the whole in every part,' have operated most disadvantageously and discouragingly to the progress of calm and dispassionate inductive inquiry into that higher law or condition upon which the power of determining the special homologies of the bones of the skeleton depends. Nevertheless the utterances of gifted spirits to whom the common intellectual storehouse is indebted for such original and suggestive generalizations as those contained in the "Program über die Bedeutung der Schädelknochen" are entitled to respectful consideration, even when they happen to be least intelligible or most counter to the conventional expressions of the current anatomical knowledge of the day; and, for my own part, I must acknowledge that reiterated attempts to detect their latent meaning have not been wholly unproductive.

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[*] "Quant à M. Oken—il déclare les pièces en question les parties écailleuses des temporaux, ou, selon son langage mystique, '*la fourchette du membre supérieur de la tête.*'"—Ossem. Foss. v. pt. ii. p. 75.—"Cet *humérus de la tête* de M. Oken devient pour M. Spix la *pubis* de cette même tête; ou, pour parler un langage intelligible, un des osselets de l'ouïe, savoir, le marteau."—"M. Spix croit aussi qu'il répond à la partie écailleuse du temporal, qu'il décore du titre d'*iléon de la tête.*"—&c. *Ib.* pp. 85, 86.

With regard, for example, to the term 'scapula capitis' applied by Oken to the tympanic bone in birds (fig. 23 and Pl. II. fig. 4, 28), it is quite possible that some appreciation of its serial homology with ribs and other modifications of the pleurapophysial element, besides that exhibited by the blade-bone, may have lain at the bottom of the expression. And, we may ask, whether the error here be not rather in the mode of stating the relationship than in the relationship itself? Had Oken, for example, said that the tympanic bone of the bird was a modified 'pleurapophysis,' or expressed by any other equivalent general term his idea of its standing in such general relation to its proper cranio-vertebral segment, his language would not only have been accurate, but might have been intelligible to Cuvier. When Oken called the 'tympanic' a 'cranial scapula' he unduly extended the meaning of the term 'scapula,' and converted it from a specific to a generic one. The tympanic is the homotype of the scapula, both being modified pleurapophyses, but each has an equal claim to its proper or specific name indicative of their respective modifications.

I am aware that Oken meant more than mere serial homology when he called the tympanic the 'blade-bone of the head': it is part of the phraseology of the hypothesis of the head being a repetition of the whole body, &c. But at the time when that anatomist wrote it was not known or suspected that the head already possessed the scapula, and that the modified pleurapophysis so called, actually appertained to a segment of the skull (fig. 5, p. 17, and Pl. II. figs. 2 and 7, 52, 51). In the terms '*femur capitis*,' '*tibia capitis*,' '*fibula capitis*,' '*pes capitis*,' applied by Oken to the parts of the teleologically compound mandibular ramus, and in those of '*ulna capitis*' and '*manus capitis*,' applied to the distal segments (21, 22) of the maxillary arch, we have not only instances of the attempt to express general relations of repetition or homology by special terms, but these modes of expressing the serial homologies of nos. 29, 30, 32, and of 21 and 22, betrays the misappreciation of the general homologies of the locomotive extremities, and their relations to the vertebral arches supporting them.

To gain an insight into whatever proportion of truth may be involved in the ideas signified by the phrases above cited, it is necessary to determine the essential nature of the parts called 'femur,' 'tibia,' 'humerus,' 'ulna,' 'manus,' 'pes,' &c., or the general homology, in short, of locomotive members, and the attempt to master this problem has been not the least difficult part of the present inquiry. Cuvier has offered no opinion, nor does he appear to have ever troubled himself with the attempt to decipher the signification of the locomotive members of the vertebrate animals; *i. e.* of what parts of the common vertebrate model they are the modifications.

Oken's idea of the essential nature of the arms and legs is, that they are no other than 'liberated ribs': "Freye Bewegungsorgane können nichts anderes als frey gewordene Rippen seyn *."

Carus, in his ingenious endeavours to gain a view of the primary homologies of the locomotive members, sees in their several joints repetitions of vertebral bodies (*tertiar-wirbel*)—vertebræ of the third degree †—a result of an ultimate analysis of a skeleton pushed to the extent of the term 'vertebra' being made to signify little more than what an ordinary anatomist would call a 'bone.'

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* Lehrbuch der Natur Philosophie, p. 330, 8vo, 1843.

† Urtheilen des Knochen und Schalengerüstes, fol. 1828.

But these transcendental analyses sublime all differences, and definite knowledge of a part evaporates in such unwarrantable extension of the meaning of terms.

It has been, however, I trust, satisfactorily demonstrated that a vertebra is a natural group of bones, that it may be recognised as a primary division or segment of the endoskeleton, and that the parts of that group are definable and recognizable under all their teleological modifications, their essential relations and characters appearing through every adaptive mask.

According to the definition of which a vertebra has seemed to me to be susceptible, we recognise the centrum, the neural arch, the hæmal arch, and the appendages diverging or radiating from the hæmal arch. The centrum, though the basis, is not less a part of a vertebra than are the neurapophyses, hæmapophyses, pleurapophyses, &c.; and each of these parts is a different part from the other: to call all these parts 'vertebræ' is in effect to deny their differential and subordinate characters, and to voluntarily abdicate the power of appreciating and expressing them. The terms 'secondary' or 'tertiary vertebræ' cannot, therefore, be correctly applied to the parts or appendages of that natural segment of the endoskeleton to the whole of which segment the term 'vertebra' ought to be restricted.

So likewise the term 'rib' may be given to each moiety of the hæmal arch of a vertebra; although I would confine it to the pleurapophyses when they present that long and slender form characteristic of the thoracic abdominal region, viz. that part of such modified hæmal or costal arch to which the term 'vertebral rib' is applied in comparative anatomy and the term 'pars ossea costæ' in anthropotomy: but, admitting the wider application of the term 'rib' to the whole hæmal arch under every modification, yet the bony diverging and backward projecting appendage of such rib or arch is something different from the part supporting it.

Arms and legs, therefore, are developments of costal appendages*, but are not ribs themselves liberated: although liberated ribs may perform analogous functions, as in the serpents and the *Draco volans*.

If then the arms or pectoral members be modified developments of the diverging appendage of the scapulo-coracoid arch†, and if this be the hæmal arch of the occipital vertebra, it follows that the pectoral members are parts of the head, and that the scapula, coracoid, humerus, radius and ulna, carpals, metacarpals and phalanges, are essentially bones of the skull.

The transcendentalism, therefore, which requires for its illustration that the maxillary arches be the arms and hands of the head, meets its most direct refutation in the fact of the diverging appendages, properly called arms and hands, belonging actually to one of the modified segments of which the head itself consists.

The head is, therefore, in no sense a summary or repetition of all the rest of the body: the skull is a province of the whole skeleton, consisting of a series of segments or 'vertebræ' essentially similar to those of which the rest of the skeleton is constituted.

Most of the phrases by which Spix‡ attempted to systematize and carry out the repetition-hypotheses of Schelling and Oken, as applied to the osteology of the vertebrate skull, may be similarly explained, and when well-winnowed some grains of truth may be recovered.

In denominating the palatine bone the 'hyoid bone of the face,' Spix endeavours to express a relation of general homology by a term which should be confined to the enunciation of a special homology: but he adds "cornui ossis hyoidei anteriori analogum," which shows an almost correct appreci-

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* Pl. II. fig. 1, *a a*.

† Ib. fig. 7, *a a*.

‡ Cephalogenesis, fol. 1815.

ation of the serial homology of the palatine bone. It answers, however (see no. 20 in figs. 1–6, Pl. II.), in the maxillary arch to the stylo-hyal or proximal element (no. 38) of the hyoidean arch, not to the cerato-hyal or hæmapophysial element (40); and it needs only to recognise the palatine as the 'pleurapophysis' of its vertebral segment, to appreciate all its true serial homologies. It might as well have been called the 'tympanic pedicle of the face,' the 'styloid process of the face,' the 'scapula of the face,' or the 'ilium of the face', according to Oken's and Spix's faulty method of expressing serial homological relations, since it holds in its vertebral segment the same place which each of the above-named bones respectively does in its segment.

So also, with regard to the term 'os faciei iliacum' applied by Spix to the mastoid (8), the error lies not only in the application of a special term to express a general homological relation, but in the supposed serial homology so expressed. Had Spix detected, in a cranial vertebra, the precise element answering to that called 'iliac bone' in a post-abdominal vertebra, yet it would have been more proper to have signified such serial homology by giving the general term applicable to such parts, as abstract vertebral elements.

The fact is, however, that the mastoid (8) is the parapophysis of its vertebra, whilst the ilium is a portion of the pleurapophysis of its vertebra; and the mastoid is serially homologous with the transverse process of a sacral vertebra (fig. 27, *p*), not with its expanded rib or 'ilium'; it is not, therefore, a repetition of the ilium in the skull. The true expression of the ideas which suggested the terms 'ilium of the head,' 'scapula of the head,' &c., will be found in the true enunciation of the serial homologies of the vertebrate skeleton.

Conclusion.

It finally remains for future inquiry, admitting the explanation of the endoskeletal archetype given in the present Essay to be the true one, whether such is the ultimate attainable generalization, or whether we may not gain an insight into the nature of the force by which all the modifications of the vertebrate skeleton, even those subservient to the majesty of man himself, are still subordinated to a common type.

We perceive in the fact of the endoskeleton consisting of a succession of segments similarly composed,—in the very power, in short, of enunciating special, general and serial homologies,—an illustration of that law of vegetative or irrelative repetition which is so much more conspicuously manifested by the segments of the exoskeleton of the invertebrata; as, for example, in the rings of the centipede and worm, and in the more multiplied parts of the skeletons of the echinoderms.

The repetition of similar segments in a vertebral column, and of similar elements in a vertebral segment, is analogous to the repetition of similar crystals as the result of polarizing force in the growth of an inorganic body.

Not only does the principle of vegetative repetition prevail more and more as we descend in the scale of animal life, but the forms of the repeated parts of the skeleton approach more and more to geometrical figures; as we see, for example, in the external skeletons of the echini and star-fishes: nay, the calcifying salt actually assumes in such low-organized skeletons the very crystalline figures which characterize it when deposited, and subject to the general polarizing force, out of the organized body. Here, therefore, we have direct proof of the concurrence of such general and all-pervading polarizing force with the adaptive or special organizing force in the development of an animal body.

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The marvellous phænomena of this development have, hitherto, been explained by two hypotheses or forms of expression—the one, as the result of 'vital properties' either peculiar to living matter or common to all, but latent in dead, matter; the other, as due to the operation of one or more 'vital principles,' vital forces, dynamics or faculties, answering to the ἰδέαι of Plato, deemed by that philosopher to be superadded to matter and mind, and which he defined as a sort of models, or moulds in which matter is cast, and which regularly produce the same number and diversity of species.

Now besides the ἰδέα, organizing principle, vital property, or force, which produces the diversity of form belonging to living bodies of the same materials, which diversity cannot be explained by any known properties of matter, there appears also to be in counter-operation during the building up of such bodies the polarizing force pervading all space, and to the operation of which force, or mode of force, the similarity of forms, the repetition of parts, the signs of the unity of organization may be mainly ascribed.

The platonic ἰδέα or specific organizing principle or force would seem to be in antagonism with the general polarizing force, and to subdue and mould it in subserviency to the exigences of the resulting specific form.

The extent to which the operation of the polarizing or vegetative-repetition-force is so subdued in the organization of a specific animal form becomes the index of the grade of such species, and is directly as its ascent in the scale of being. The lineaments of the common archetype are obscured in the same degree: but even in Man, where the specific organizing force has exerted its highest power in controlling the tendency to type and in modifying each part in adaptive subserviency to, or combination of power with, another part, the extent to which the vegetative repetition of segments and the archetypal features are traceable indicates the degree in which the general polarizing force may have operated in the arrangement of the parts of the developing frame: and it is not without interest or devoid of significance that such evidence should be mainly manifested in the system of organs in whose tissue the inorganic earthy salts most predominate.

With regard to the 'adaptive force,' whatever may be the expressions by which its nature and relations, when better understood, may be attempted to be explained, its effects must ever impress the rightly constituted mind with the conviction, that in every species "ends are obtained and the interests of the animal promoted, in a way that indicates superior design, intelligence and foresight; but a design, intelligence and foresight in which the judgement and reflection of the animal never were concerned; and which, therefore, with Virgil, and with other studious observers of nature, we must ascribe to the Sovereign of the universe, in whom we live, and move, and have our being*."

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* See Barclay, Life and Organization, 8vo, 1822.

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Ibid. p. 516): but he also ascribes a distinct petrosal
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d. p. 507), which must be either part of the exoccipi-
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ntere Abtheilung des Schläfenflügels (in monotremes),
"Felsentheil desselben (os petrosum)," Bojanus.
eine Flügel des Keilbeins," Bojanus; "Vordere Schla-
Köstlin.
bein, Köstlin.
oideum, Bojanus and Köstlin.
transversum," Köstlin.
enktheil des Schläfensbein," Köstlin; "Paukenring-
Bojanus.
henflügel des Keilbein, Bojanus.
fortsatz, Köstlin; Flügelbein, Bojanus.
erches sur les Poissons Fossiles, 4to, t. i. 1843.
orporis humani Fabricâ, 8vo, 1794.

AL HOMOLOGIES.

GEOFFROY (1824)[9].	CARUS (1828)[10].	
Cycléaux des VIème et VIIème vertèbres[10].	Grundbein oder Wirbelkörper (Unterer paralleler Tertiarwirbel) des I. Schädelwir-	Nos.[1] 1.

DESCRIPTION OF PLATES.

PLATE I.

In each of the figures the nos. upon the bones answer to those in the first column of Table I. and Pl. II., except where otherwise expressed.

Fig. 1. Skull of a Maccaw (*Calyptorhynchus*), see pp. 41, 42, 61.
Fig. 2. Skull of a Sciænoid fish, (*Pristipoma*).
ol. Foramen in nasal neurapophysis (prefrontal) for olfactory nerve.
Fig. 3. Section of a skull of a Siluroid fish, (*Bagrus*).
c. Centrum of ordinary abdominal vertebra.
n. Neural arch of ditto. c_5. Centrum of 5th corporal vertebra.
ch'. Portion of peripheral or cortical part of the same centrum, forming the posterior aperture of the aortic canal.
n_5. Neurapophysis of the same vertebra, separately perforated by the motor and sensitive roots of the spinal nerve.
c_4. Centrum of 4th vertebra.
c_4, *ex.* External or cortical development of same centrum.
n_4. Neurapophysis, and p_4 parapophysis, of same vertebra.
c_3. Centrum of 3rd vertebra.
c_3, *ex.* External or cortical development of same centrum.
n_3. Neurapophysis, and p_3 parapophysis, of 3rd vertebra.
c x. Centrum of 2nd or axis vertebra.
c x, ex. External or cortical development of same centrum.
n x. Neurapophysis of axis. *ns, x.* Neural spine of axis.
p x. Parapophysis of axis.
c a. Centrum of 1st corporal vertebra or 'atlas.'
c a, ex. External or cortical development of same centrum.
n a. Neurapophysis of atlas separated from its centrum.
p a. Parapophysis of atlas.
c h. Anterior aperture of aortic canal, formed by the development and coalescence of the inferior cortical portions of the bodies of the five anterior vertebræ of the trunk.
c o. Centrum of occipital vertebra.
in. Internal part, and *ex* external or cortical part of the anterior prolongation of the same centrum.
n o. Neurapophysis of occipital vertebra; *s* is a continuation of the same bone, forming its otocranial plate.

ns, o. Neural spine of occipital vertebra.

c p. Centrum of parietal vertebra: it appears to consist of the denser cortical part only.

n p. Neurapophysis of parietal vertebra: the hinder figure 6 marks the otocranial plate which combines with 2, 8 (occipital parapophysis), and 12 (parietal parapophysis), in forming the chamber for the cartilaginous petrosal or acoustic capsule.

c f. Centrum of frontal vertebra, connate with *c p.*

n f 10. Neurapophysis of frontal vertebra.

ns, f 11. Neural spine of ditto.

c n. Centrum (represented by its cortical part) of nasal vertebra.

n n. Neurapophysis of ditto: it coalesces with its fellow at the median line.

ns, n. Neural spine of nasal vertebra: it coalesces anteriorly with the centrum; closing there the neural canal.

tr. Intervertebral foramen between parietal and frontal neurapophysis, for the exit of the trigeminal nerve.

op. Foramen in frontal neurapophysis, for the exit of the optic nerve.

ol. Foramen in nasal neurapophysis, for the exit of the olfactory nerve.

The two foramina for the nerves of the epencephalic segment are below the letters *n o*: beneath the foramina is the 'sinus auditorius.'

Fig. 4. Upper view of part of the preceding cranium: chiefly to show the modifications of the corporal parapophyses, *p* 6 to *p a*, as they approach the region of the cranial vertebræ: here *p o* is the occipital parapophysis; *p p* the parietal parapophysis, and *p f* the frontal parapophysis. *ns, f* the permanent fontanelle in the bifid frontal spine. *pl* the occipital pleurapophysis; the letters indicate the part answering to the tubercle of the human thoracic rib, which here bifurcates and articulates with both the parapophysis of its own segment (4) and with that of the preceding segment (8). The numbers give the special homologies of the bones, according to Table I.

Fig. 5. Section of the skull, atlas and axis of a sword-fish (*Xiphias Gladius*).

c x. Centrum of the axis vertebra.

n x. Neurapophysis of ditto.

s x. Neural spine of ditto.

c a. Centrum of the atlas.

n a. Neurapophysis of ditto.

s a. Neural spine of ditto.

c o 1. Centrum of the occipital vertebra.

n o. Neurapophysis of ditto.

n s o. Neural spine of ditto.

p o. Parapophysis of ditto.

c p 5. Centrum of parietal vertebra.

n p. Neurapophysis of ditto.

c f 9. Centrum of frontal vertebra.

n f. Neurapophysis of frontal vertebra.

f. Medullary part of ditto.

c n. Centrum of nasal vertebra.

ns, f. Neural spine of frontal vertebra.

n n. Neurapophysis of nasal vertebra, which, by its cellular structure, resembles that, called ethmoid, in mammals.

ns, n. Spine of nasal vertebra.

Fig. 6. Occipital and five following vertebræ of *Fistularia tabacaria*.

c 5. Centrum of fifth corporal vertebra.

p 5. Parapophysis of ditto.

such appendages of the occipital vertebra, which undergo modifications closely analogous to those of the appendages of the pelvic segment or 'hind limbs.' And inasmuch as in one class the pelvic appendages, with their supporting hæmal arch, are detached from the rest of their segments, and subject to changes of position (fig. 2, V, V′, V″), so also in other classes the appendages of the occipital segment are liable to be detached with their sustaining hæmal arch, and to be transported to various distances from their proper centrum and neural arch.

The head therefore is not a virtual equivalent of the trunk, but is only a portion, *i. e.* certain modified segments, of the whole body.

The jaws are the modified hæmal arches of the first two segments; they are not 'limbs' of the head.

The different elements of the primary segments are distinguished by peculiar markings:—

the neurapophyses by diagonal lines, thus:—▨
the diapophyses by vertical lines:—▥
the parapophyses by horizontal lines:—▤
the *centrum* by decussating horizontal and vertical lines:— ▦
the pleurapophyses by diagonal lines:—▧
the hæmapophyses by dots:—░
the appendages by interrupted lines:—┅
the neural spines and hæmal spines are left blank.

In certain segments the elements are also specified by the initials of their names, as in the third segment in fig. 1, and the fourth in fig. 2, for example:—

ns is the neural spine.
n is the neurapophysis.
pl is the pleurapophysis.
c is the centrum.
h is the hæmapophysis.
hs is the hæmal spine.
a is the appendage.

Fig. 1. Ideal pattern or archetype of the vertebrate endoskeleton, as shown in a side view of the series of typical segments or 'vertebræ' of which it is composed, with the commencement indicated at the two ends of those modifications, which, according to their kind and extent, impress class-characters upon the type.

The four anterior neurapophyses, 14, 10, 6, 2, give issue to the nerves, the terminal modifications of which constitute the organs of special sense.

The first or foremost of these is the organ of smell (12, 10), always situated immediately in advance of its proper segment, which becomes variously and extensively modified to inclose and protect it.

The second is the organ of sight (17), lodged in a cavity or 'orbit' between its own and the nasal segment, but here drawn above that interspace.

The third is the organ of taste, the nerve of which (gustatory portion of the trigeminal) perforates the neurapophysis (6) of its proper segment (*vertebra, parietalis* seu *gustatoria*), or passes by a notch between this and the frontal vertebra, to expand in the organ which is always lodged below in the cavity called 'mouth,' and is supported by the hæmal spine (41, 42) of its own vertebra.

The fourth is the organ of hearing (16), indicated above the interspace between the neurapophysis of its own (occipital) and that of the antecedent (parietal) vertebra, in which it is always lodged; the surrounding vertebral elements being modified to form the cavity for its reception, which I have called 'otocrane.'

The mouth opens at the interspace between the hæmal arches of the anterior and second segment; the position of the vent varies (in fishes), but always opens behind the pelvic arch (Pv) when this is ossified.

Outlines of the chief developments of the dermoskeleton, in different vertebrates, which are usually more or less ossified, are added to the endoskeletal archetype*; as, *e.g.* the median horn supported by the nasal spine (15) in the rhinoceros; the pair of lateral horns developed from the frontal spine (11) in most ruminants; the median folds (DI, DII) above the neural spines, one or more in number, constituting the 'dorsal' fin or fins in fishes and cetaceans, and the dorsal hump or humps in the buffaloes and camels; similar folds are sometimes developed at the end of the tail, forming a 'caudal' fin, C, and beneath the hæmal spines, constituting the 'anal' fin or fins, A, of fishes, or the subcaudal dermo-adipose tumour of the Cape-sheep.

Fig. 2. Typical skeleton of a fish (class *Pisces*). The plane of the anterior hæmal arch (20, 21, 22) is here raised to parallel with the axis of the trunk, and its apex or spine (22) is modified and developed so as to articulate with the neural spine (15) of the same segment, which thus becomes closed anteriorly; both 22 and the hæmapophysis 21 are developed downwards and backwards in relation to the protractile and retractile motions of the arch; and for the purpose of associating these motions with corresponding ones of the succeeding hæmal arch, the diverging appendage is subdivided (23 and 24) and developed so as to articulate with the pleurapophysis (28) of the next arch; a rudiment of an appendage (26) is attached in some fishes to the hæmapophysis (21) of the nasal segment, but it will be observed that no new element is added to the hæmal arch; and, although the *Lepidosteus* offers an exceptional instance of subdivision of the pleurapophysis (21), that kind of modification is usually restricted to the diverging appendage.

In the next segment the hæmal arch has been the seat of unusual growth, but retains more of its normal position and attachments. Its weight and that of the appendages it supports have required an extension of the proximal articulation of its pleurapophysis (28 *a*) from its proper parapophysis (12) backwards to the next parapophysis (8); and the pleurapophysis itself is subdivided into two, three, or four overlapping pieces for the final purpose explained in p. 112; but it is evident that no new element has been intro-

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* I have used this word here, and in the 'Report of the British Association for 1846,' pp. 169, 241, in the sense which it bears in such classical works of our own language as Glanville's Scepsis and Watts's Logic, and agreeably with its definition in Johnson's and other dictionaries, as the original or pattern of which any resemblance is made: and as equivalent to the terms 'general type' and 'fundamental type' as they occur in my "Lectures on the Vertebrate Animals," 8vo. 1846, p. 41, and *passim*.

In the 'Comparative Osteology' of Joseph Maclise, Esq., in which the author's views of the homologies of the bones of the trunk are illustrated by fifty-four beautiful plates, many of which are peculiarly well adapted to convey clear ideas of those relations in the human skeleton, the word 'archetype' is used as synonymous with 'unity.' "Unity under metamorphosis is an archetype plus quantity, being subjected to the law of proportion. Unity and the archetype may hence be regarded as one and the same thing, consequently the metamorphoses and proportionals are also understood as the products of unity or the archetype." —Remarks on plate 15. And again the author says, "Unity, or the archetype, is a name which may be applied to characterise that whole structure which is capable of undergoing metamorphosis or subtraction through all degrees of quantity severally equal to all those proportional forms which stand in series with itself."—Remarks on plate 16.

duced, because the extremities of the subdivided pleurapophysis (28 *a* and 28 *d*) retain their normal connections, the one with the parapophysis (12), the other with the hæmapophysis (29, 30). This element is also subdivided, for the same final purpose as the pleurapophysis; and its squamous union with the hæmal spine (32) is retained. Yet the connections of 29 with the condyle of the pleurapophysis and of 32 with its fellow, forming the free apex of the inverted arch of the second segment, show that the complexity is the result of mere (teleological) subdivision, and that no new part has been added to the typical elements as exhibited in the archetype* (fig. 1, 28–32); every anatomist has recognised the bones so numbered in the fish as the homologue of the single (undivided or anchylosed) bone forming the lower jaw (29–32) of the mammal (fig. 5) and of man (fig. 6). In addition, therefore, to change of shape and proportion, the parts of the archetype may be modified by division and subdivision. And in this respect the pleurapophyses (28) and hæmapophyses (29, 30, 31) of the fish deviate further from the archetype than the same parts do in the warm-blooded vertebrates. Herein is manifested the early divergence to a special form for the lowest class, which the higher classes do not assume in passing towards their own types. The diverging appendages are the seat of such excess of subdivision with special development of the divided parts, as best to countenance the idea of a superaddition of new parts to the typical element; yet the most essential character of the diverging appendage is retained under its extremest modification, as where it forms the wing of the bird or the arm of man; viz. its connection by one extremity to a hæmal arch, and the free projection of the opposite subdivided extremity, carrying out with it a fold of integument. With regard to the diverging appendage of the hæmal arch of the second segment, its modifications are arrested at different stages of departure from the simple archetypal form (34–37, fig. 1), as explained at pp. 66 and 112. The most common modification in bony fishes is that shown in fig. 2, where it is divided into two segments, and the second segment into three pieces (35, 36, 37), usually broad and flat, for the office explained at p. 112.

The parietal segment, or third counting backwards, has the hæmal arch (38–41) detached from its proper supporting parapophysis (8) by the backward development of 28 *a* of the preceding segment. This is the first example of another modification, viz. that of dislocation, sometimes accompanied by great change of place, which has tended most to obscure the essential nature of parts, and their true relations to the archetype. The principle of subdivision still manifests itself in the elements of the hæmal arch, especially in its spine, 41–43; and in a greater degree by a vegetative repetition of the 'appendage' (44), without departure from its primitive ray-like form.

The pleurapophysis of the occipital segment (50, 51) is divided into two, and its proximal end is usually bifurcate in fishes, articulating like the normal ribs of higher animals, by a 'head' and a 'tubercle' to two points of the neural arch of its segment.

Almost every stage of development and departure from the primitive type is manifested by the diverging appendage (54–57) up to the extent of modification attained by the typical osseous fish. The proximal segment is divided into two pieces (54 and 55), the next segment into four or more (56), and the last segment into a greater but variable number of pieces, retaining the elementary form of rays.

The Lepidosiren (fig. 7) is eminently instructive by the retention in the occipital vertebra of the primitive condition of the appendage, as shown in the archetype (fig. 1, 53–57), modified only by segmentation of the ray. The pleurapophysis of the arch (51) likewise retains its simple cylindrical form, and is articulated to its centrum, like the other ribs of the Lepidosiren, by an undivided head.

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* See note, p. 177.

The hæmal arch of the fifth segment (first of the trunk) is commonly detached from its centrum and neural arch in fishes, without being displaced backwards. The pleurapophysis (*pl*) is short and simple, sometimes expanded; the hæmapophysis (52, *h*) is simple, long and slender. When this arch supports an appendage it is a simple diverging ray.

All the succeeding abdominal segments of the fish have their hæmal arches incomplete by bone; the hæmapophyses and spines retaining the primitive fibrous condition. The pleurapophyses of most support diverging appendages in the form of simple undivided bony rays.

A part of the hæmal arch of a post-abdominal (pelvic) segment is ossified (63), and supports a more complex appendage (65) in the form of one, two or more jointed rays, which project beyond the surface and are enveloped by a fold of skin forming the 'ventral' fin, V, making a pair with the one on the opposite side. This partially ossified hæmapophysis articulates with its fellow by its anterior apex, forming a 'symphysis ischii' seu 'pubis'; and, in some fishes called 'abdominal,' it is connected to its proper pleurapophysis (62) by an aponeurosis representing its unossified continuation.

The remarkable degree to which one and the same part may be subject to the modification of change of position, is strikingly exemplified in this lower portion of the pelvic arch with its appendages in fishes. It may be moved forwards, so that the symphysis of the pelvic arch is brought into connection with that of the scapular arch; when, according to the length of the ossified parts of the pelvic hæmapophyses, the species is either 'thoracic,' as when the ventral fins are at V′, or 'jugular,' when they are advanced to V″. The universally acknowledged and long recognised special homology of the hæmal arch and appendages of the pelvic vertebra, as the 'ventral fins' of fishes, under these changes of position, prepare us for the recognition of an analogous modification of the hæmal arch and appendages of the occipital vertebra in the higher classes of vertebrata.

Beyond the abdomen the osseous and aponeurotic parts of the hæmal arches rapidly contract; the progressively elongated parapophyses usually bend down and complete the inverted arch by their apical coalescence; sometimes distinct pleurapophyses continue to form these arches; sometimes these elements may be traced, anchylosed with their fellows of the opposite side, and with the coalesced extremities of the parapophyses. The bodies of a certain number of the terminal segments coalesce together in the typical osseous fishes, and support several neural and hæmal arches and spines, usually more or less expanded, and forming the basis of the caudal fin, C.

The ossified parts of the dermal median and symmetrical folds, constituting the dorsal (DI, DII), the anal (A), and caudal (C) fins, are added to the endoskeleton in fig. 2; *in* are the interneural spines; *dn* the dermoneural spines; *ih* the interhæmal spines; *dh* the dermohæmal spines; these form no part of the true vertebral skeleton, and are peculiar to fishes. The diagram of the modified cranial segments is not complicated by the outlines of the sense-capsules or mucodermal bones; the latter are shown in fig. 2, r_1, r_2, Plate I.

Thus, compared with the archetypal figure, the endoskeleton of the fish deviates by excess of development, manifested chiefly in the diverging appendages of the four anterior or cranial segments, and by arrest of development in most of the other segments; but the principle of polaric or vegetative repetition greatly prevails, and more of the segments resemble one another than in any of the higher classes.

Fig. 3. The Crocodile is here taken as the type of the class *Reptilia*.

The hæmal arch of the anterior segment is now firmly fixed by excessive development, chiefly of its hæmapophyses (21), which have extended their attachments to all the elongated elements (13, 14 and 15) of their own neural arch. The diverging appendage (24) from the pleurapophysis (20) fixes the arch extensively to the centrums of the second and third segments: the appendage from the hæmapophysis (21) bifurcates; one branch, divided into two pieces (26 and 27), connects the arch with the pleurapophysis (28) of the next segment; the other branch (25) extends the attachment to the parapophysis (12) of the same segment, and also to the appendage (24) of its own arch.

The pleurapophysis (28) of the frontal segment is undivided; it is represented as displaced and depressed; but in nature it still retains a small part of its connection with its proper pleurapophysis (12), although it is developed backwards so as chiefly to articulate with that (8) of the following segment: it supports no diverging appendage. The hæmapophysis (29–31) is more subdivided than in fishes, in relation to functions explained in pp. 122, 123.

The excess of development of the hæmal arch of the frontal vertebra is compensated by the defect of development of that of the parietal one (40, 41); and this constitutes the next great additional step in the deviation from the archetype. Only the hæmapophyses (40) are ossified: the hæmal spine, though much expanded and flattened, remains cartilaginous, and the pleurapophysis is represented by a feeble ligament. The whole arch is detached and displaced backwards, and its diverging appendages cease to be developed.

The tendency to retrogradation manifested by the preceding hæmal arches is carried out to a striking extent in that (51, 52) of the occipital segment (the fourth counting backwards): it overlaps the homotypal arches of the 8th to the 11th segments of the trunk: the ossified portions of both its constituent element, 51 and 52, are simple; the hæmal spine 52′ is prolonged backwards. The diverging appendage manifests, in comparison with that in the fish, an additional segment (53), which is single; the segment of two pieces (54 and 55) is now the second. The rays of the distal segment are reduced to five in number, which is never afterwards exceeded in the vertebrate subkingdom. The dislocation and retrogradation of the posterior hæmal segment of the skull form the second chief additional feature of departure from the archetype, as compared with the skeleton of fishes. The third well-marked modification is the development of an inferior (cortical) portion of the body of the atlas (*ca*, *x*), distinct from the main part of that centrum (*ca*), which coalesces with that of the axis, and is commonly called its 'odontoid' process (see p. 93).

The nine segments that succeed the head resemble those of fishes in the non-ossification of the hæmapophyses and hæmal spines, but deviate further from the archetype by the minor development of the pleurapophyses. These progressively elongate to the 12th vertebra, where the hæmal arch is completed by a hæmapophysis and hæmal spines.

The hæmapophyses are not so completely ossified as the pleurapophyses, and they are divided from these by the interposition of cartilaginous pieces, *a a*; these pieces may be regarded either as dismemberments of the hæmapophyses, or as unossified parts of the pleurapophyses. The diverging appendages (*a*, *a*) are usually cartilaginous.

Beyond the 21st segment of the trunk* the pleurapophyses usually cease to be represented either by bone or cartilage: but the partially ossified hæmapophyses are continued to those of the pelvic segments, 64 and 63, *h*. In these segments the pleurapophyses reappear, and are divided into two parts, like those in the thorax: the proximal portions (*pl*, *pl*) are short and thick; the distal portions have either coalesced into one broad and thick plate (62 *pl*), or the distal portion of one pleurapophysis is still more remarkably developed and takes the place of two: this question is discussed at pp. 160, 161. The two hæmapophyses (63, 64) are distinct and well-ossified. The diverging appendage (65–68) has been subject to the same kind and amount of development as that of the scapular arch (53–57). The first steps in the progression of this metamorphosis from the primitive type is shown in the *Lepidosiren* (fig. 9), and the *Proteus* (fig. 10). The modification of the pelvic segments and their appendages in the reptile forms another prominent feature of deviation from the archetype. The pleurapophyses are continued, progressively shortening, attached to the diapophyses of a certain number of the vertebræ that succeed the sacrum: the hæmapophyses are no longer attached to their extremities but are directly articulated to the central elements, with a slight degree of displacement, whereby they articulate to another segment as well as to their own. The mode and degree of departure from the archetype are now such that different series of vertebral segments may be classed into groups, with distinctive characters and names:—

The first four segments, by the fixed union of their neural arches, as *cranial* (Cr), under the collective name of 'skull.'

The next nine segments, moveably articulated, and with free or 'floating' pleurapophyses, as *cervical*, C, forming collectively the region called 'neck'.

The succeeding nine segments with ossified and moveable pleurapophyses and hæmapophyses, as *dorsal*, D, forming the 'back,' 'thorax' or 'chest.'

The three following moveable vertebræ, without free bony pleurapophyses, as *lumbar*, L, forming the 'loins.'

The next two vertebræ, immoveably united, and with modified and much-developed hæmal arches and appendages, are called *sacral*, and collectively 'pelvis and hind limbs.'

All the other segments are '*caudal*' and constitute the 'tail.'

The hæmal arch (51, 52) with the developed appendages (53–57 *a*) detached from the occipital vertebra, may require to be specially noticed in this summary of the parts of the endoskeleton, as from the circumstance of its com-

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* According to Cuvier, the pleurapophyses cease to appear after the 20th trunk-vertebra in the *Crocodilus biporcatus*, and after the 19th in *Alligator lucius*. I allude to these differences for the purpose of remarking that the conformity of organization is greater than would appear at first sight from the formulæ of the vertebræ of the different species of crocodile cited in the Table at p. 220, tome i. Leçons d'Anatomie Comparée, 1835. The number of vertebræ from the atlas inclusive to the sacrum is the same in each species, as will be seen by the following extract:—

	Cervical.	Dorsal.	Lumbar.		
Crocodile à deux arêtes	7	13	4	=	24
Crocodile du Gange	7	14	3	=	24
Caiman à mus. de brochet	7	12	5	=	24

The difference in the dorsal and lumbar series depends merely on the ossification or otherwise of the pleurapophysial tendons or fibrous basis attached to the diapophyses of the 20th, 21st and 22nd vertebræ.

A slight change in the form and size of the pleurapophysis is all that distinguishes the first dorsal from the last cervical vertebra in the Cuvierian Table.

monly remote position from its proper segment, it may not have been thought of as a part included in the first class of vertebræ constituting the skull.

Many striking and extreme deviations from the archetype are manifested in the skeleton of the more aberrant forms of the reptilia. The number of moveable trunk-segments is reduced to the minimum in the *Batrachia* (*e.g.* 7 in *Pipa*), and increased to the maximum in the *Ophidia* (422 in *Python*). At first view the principle of vegetative repetition seems to have exhausted itself in the long succession of incomplete vertebræ which support the trunk of the great constrictors: but by the endless combinations and adjustments of the inflections of their long spine the absence of locomotive extremities is so compensated that the degraded and mutilated serpent can overreach and overcome animals of far higher organization than itself: it can outswim the fish, outrun the rat, outclimb the monkey, and outwrestle the tiger; crushing the carcase of the great carnivore in the embrace of its redoubled coils, and proving the simple vertebral column to be more effectual in the struggle than the most strongly developed fore-limbs with all their exquisite rotatory mechanism for the effective and varied application of the heavy and formidably armed paws. And whilst the vertebral column of the ophidian order exhibits the extreme of flexibility, that of the chelonia manifests the opposite extreme of rigidity: back, loins and pelvis constitute one vast sacrum, or rather abdominal skull, but a skull subordinated chiefly to the lodgment and defence of a much-developed hæmal system, and in which the pleurapophyses, hæmapophyses and their spines repeat the same modification of great expansion and fixed union by marginal sutures, which the neurapophyses and spines undergo in the cranium of the higher vertebrates. The well-known determination of the ordinary elements of the typical vertebra in the thoracic-abdominal segments of the tortoise need not here be discussed (see pp. 100, 101): but it is, perhaps, worthy of repetition that the neurapophyses exhibit the modification of change of position, like that which has been described in the sacrum of the bird; being shifted from their own centrum over one half of the next centrum, thus adding to the strength and elasticity of the whole osseous vault (see p. 95). The confluence of the neurapophysis (14) with its own moiety of the neural spine (15) has already been noticed (p. 124) in the anterior segment of the cephalic skull of most chelonia. I may here add that the typical condition of the hæmal (maxillary) arch of the same segment is well shown in the *Emys expansa*. The pleurapophyses (palatines) meet at the base of the cartilaginous vomer, above and behind the posterior nares, sweep outwards and downwards, give attachment to the hæmapophyses (maxillaries) which advance and converge, and the arch is closed below the nasal passage by the hæmal spine (premaxillary). Cut through the junction of the hæmapophyses with the neurapophyses (prefrontals), and with the diverging appendages (malars), and the inverted arch is then suspended by its proper piers, the pleurapophyses or palatines.

In the connation or coalescence of the neurapophyses and spines forming the parietal and frontal neural arches in the ophidian and some chelonian reptiles, we perceive a return to the common constitution of those arches in the vertebræ of the trunk, in which the permanent separation of the neural spine from the neurapophyses occurs as a rare exception.

In the class-skeleton (*Aves*) represented in fig. 4 the archetype is further departed from than in the typical reptilia; and when the general form of this diagram is contrasted with that of the first figure, the power of demonstrating the fundamental agreement which reigns throughout, and which is equally manifested in the comparison of figure 4 with those of the piscine and reptilian skeletons, affords a most striking proof of the unity of plan which pervades the whole series.

As compared with the crocodile (fig. 3) the proportions of the hæmapophysis (21) and spine (22) of the anterior segment are reversed; there is a return towards the condition of the parts in fishes (fig. 2); the strength of the arch being chiefly due to the great development and extensive connections of 22, which usually sends a process upwards and backwards between the divided neural spine (15) of its own to that (11) of the next segment. The pleurapophysis (20) has often a slender rib-like form, and the appendages retain the form of bony rays. That (24) from the pleurapophysis is simple; that (26, 27) from the hæmapophysis is divided in the embryo-bird: both concur in attaching the hæmal arch of the anterior segment to the pleurapophysis of the second segment. The neurapophyses of the anterior segment coalesce and form a single vertical bone, slightly expanded above and sometimes appearing anterior to the frontal.

The hæmal arch of the second segment is detached from its neural arch; and, although its proper parapophysis (12) sometimes joins the next one (8), yet this exclusively supports, in birds, the pleurapophysis (28) of the frontal segment. The hæmapophysis is developed, as in the reptile, from several centres (29, 29′, 30′, 31), but these coalesce with each other and with the hæmal spine, 32, to form the single bone called lower jaw in most birds.

The hæmal arch (40–46) properly appertaining to 8—the parapophysis of the parietal segment—is detached from it, and freely suspended, somewhat retrograded in position beneath the next segment: its development has suffered as marked an arrest as in the crocodile.

The hæmal arch, with its appendages of the hindmost segment of the skull, is displaced backwards to a greater extent than in the reptile.

The pleurapophysis, 51, retains the form of a long, flat, slightly-arched rib: the hæmapophysis (52) is straighter and stronger. There are birds (*Apteryx*, e. g.) in which this arch is arrested at almost as early a stage of growth as is the antecedent (hyoid) arch of the skull. The elements of the neural arches of the skull, 1–15, early anchylose together in most birds, with the exception of the centrum (13) of the foremost segment, which more commonly coalesces with the pleurapophyses (20) of its hæmal arch.

The size of the brain now demands a modification of the neural arches superadded to those which they present in the cold-blooded vertebrates, and occasions a marked difference in the form of the skull: it is important to note how this is obtained. The nature of the modification is well shown in the young of those large birds which are devoid of the powers of flight. No new bone is introduced to increase the cranial walls and give the cavity its due capacity; this is gained by excess of growth of common and constant elements; and, as has been shown in pp. 126–128, those furthest from the centrum (3, 7, 11) are the chief seat of such excess. With regard to the neural spines of the frontal and parietal vertebræ, it is accompanied by a temporary bipartition, the ossification commencing from two lateral centres in each; but the halves soon coalesce with each other and with their sustaining neurapophyses (2, 6; 10).

In those segments which, from the brevity and free termination of the pleurapophyses, may be called 'cervical,' the elements of the neural arch and also the pleurapophyses early anchylose together in each segment, converting it into the single bone, called in comparative osteology a 'vertebra,' and these vertebræ are remarkable for their great number in most birds; and consequently the neck is as remarkable for its great length and flexibility. The detached hæmapophyses (58) of one of these vertebræ, (which vertebra, by the analogy of the fish (fig. 2, *ss*), should be the *atlas*,) commonly coalesced together at their distal ends forming a bony arch, like a slender edentulous lower jaw, have followed the hæmal arch of the occipital vertebra (*s1*, *ss*) in its retrograde course, though not quite to the same extent. These mutually anchylosed hæmapophyses (*ss*) forming the bone, called 'furculum' in ornithotomy, are generally the only pair of ossified cervical hæmapophyses. If, however, we define the cervical vertebræ, as in the crocodile, by their mobility and the free termination of their pleurapophyses, we may then recognise in some birds the detached hæmapophyses of the last cervical vertebra attached, as at *h*, to those of the succeeding segment: this structure may be observed in the common goose (*Anser palustris*). The pleurapophyses of the posterior cervical vertebræ are free, and rapidly elongate. The hæmapophyses of the segments with complete hæmal arches are bony, and are commonly defined as 'sternal ribs', their pleurapophyses being called 'vertebral ribs,' agreeably with the restricted anthropotomical meaning of the term 'vertebra.' These pleurapophyses support bony appendages (*a a*), which serve, like those of the foremost hæmal arch of the skull, to connect their own arch to the next and associate them together in movement*. After six or seven segments with these typical hæmal arches come others with shorter pleurapophyses terminating freely, not reaching their hæmapophyses, one of which, ossified, is shown in the diagram at *h'*, adhering by its distal end to the preceding hæmapophysis and terminating freely above. These 'floating sternal ribs' are more numerous in the crocodile (fig. 3, *h'*). The hæmal spines of the dorsal segments with complete hæmal arches, become the seat of the most extensive and characteristic modifications of the avian type of skeleton. They are greatly extended in breadth, and, like the correspondingly expanded neural spines of the cranial vertebræ, are developed from two lateral moieties; but the individual spines, indicated by dotted lines in the diagram (*se*), are not ossified from separate centres, but continuously, so that the hæmal spines of six or eight vertebræ are at first represented by a pair of osseous plates. A cartilage is usually extended vertically from their median junction, which, when ossified, forms a strong crest or 'keel' (*se'*). The hæmal spine of the scapular arch (*ss'*) is sometimes ossified from a proper centre; as is also a piece prolonging the series posteriorly: but all soon coalesce into one bone called 'sternum.' The anterior portion, *ss'*, has received the name of 'episternum', the median keel, *se'*, that of 'entosternum,' the posterior piece, which sometimes remains cartilaginous, that of 'xiphisternum.' In the terrestrial birds incapable of flight the keel or 'entosternum' is not developed: in the rest of the class the extent of this part and of the ossified portion of the body of the sternum bears a direct ratio to their power of flight; the peculiar modification of these extreme elements of the dorsal segments being governed by the size of the muscles moving the wings.

The next great deviation from the typical standard, peculiar to birds, is the great extent of the vertebral axis which is embraced by the enormously developed pelvic pleurapophyses, *ss*, and the unusual number of segments which, being thus deprived of reciprocal motion, grow together and form, according to this character, the bone or region called 'sacrum.' In investigating the structure of this part of the endoskeleton in the embryo-bird, the neural arches are found to manifest a change of position analogous to,

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* These appendages are not the result, as has been supposed, of a bifurcation of the vertebral rib: they are independent pieces originally in all birds, and retain their individuality in some, *e.g.* apteryx, penguin, with proper muscles for their elevation and depression—potential homotypes of the flexors and extensors of more developed limbs.

though less extensive than, that of certain of the hæmal arches of more anterior segments (s1–s2, *e. g.*): the results of this analysis are fully detailed at pp. 95 and 159. Most of the pleurapophyses of the sacral vertebræ are stunted in their growth, which may literally be said to be stopped by the pressure upon their extremities of the overgrown distal portion of one of their homotypes, forming the bone called 'ilium' (62, *pl*). But one or two of the pleurapophyses at the anterior part of the series (*pl*) escape from beneath the 'ilium' to terminate freely at some distance below it: these are usually bifurcate at their proximal ends, and moveably articulated to their anchylosed centrums and diapophyses: the shorter anchylosed sacral pleurapophyses have simple proximal ends and articulate in the embryo to the interspace between their own and the adjoining centrum, as shown in the cut 27, *pl*, to which they soon become anchylosed.

The contemplation of the modifications of the different natural segments in the trunk of the bird, particularly the freedom of some elements and the fixation of others, strongly impresses on the mind the purely artificial character of the regions of the spine which have been transferred from anthropotomy into the anatomy of the vertebrate animals. Thus Cuvier declares, "Il n'y a point de vertèbres lombaires proprement dites*." And a later author:—"Die Wirbel zerfallen in Hals- Rücken- Kreuzbein- und Steisswirbel; eigentliche Lendenwirbel sind gewöhnlich nicht zu unterscheiden."

Cuvier's negation of proper lumbar vertebræ in birds of 1799 is reproduced in succeeding systems and handbooks of comparative anatomy down to the latest by Siebold and Stannius, *e. g.* of 1846. But the student of anatomy in its wider acceptation will understand that the segments homologous with those included under L in fig. 3, are by no means wanting in fig 4, but only otherwise modified.

It may be regarded as highly probable at least, from the striking points of agreement which are observable in the organization of the crocodile and of the bird, that, counting backwards from the first 'dorsal' in figs. 3 and 4, the next twenty segments are homologous in both. But, in the bird, those that answer to the three or four last dorsal vertebræ in the crocodile are anchylosed together, and the last of these had its pleurapophyses modified to form abutments against the elongated ilia. The next three segments, answering to the lumbar in the crocodile, are modified as in the last 'dorsal.' The two following segments similarly modified will answer then to the two sacral vertebræ of the crocodile, and anchylosis extends backwards so as to include two or three vertebræ homologous with the anterior caudals in the crocodile. This appears to be the true interpretation of the enormous 'sacrum' of the bird; it is not merely 'lumbo-sacral' but 'dorso-lumbo-sacro-caudal', including as it does representatives of each of those classes of vertebræ in the crocodile, but which have lost the artificial characters that distinguished them in that nearest allied existing vertebrate. The special homologies are indicated by the letters D, L and S.

The characters of the regions of the vertebrate skeleton are, as already remarked in reference to the crocodile, artificial, and are used for the sake of convenience in describing and comparing the vertebræ of different species. Those, therefore, are the best which are the most constant and most readily applicable in any given class. Proceeding to assign such to the bird, as in the crocodile, unbiassed by anthropotomical characters of the vertebral regions, all those may be called 'cervical' in the bird that extend from the skull to the first vertebra with the hæmal arch complete, and those dorsal that extend from that vertebra inclusive, to the first vertebra embraced by, and anchylosed to, the iliac bones. One usually finds in the falcons, the gallinaceous birds and in some waders, five or six of the centrums and neural arches of the dorsal vertebræ anchylosed into one mass, a single free centrum usually intervening between this mass and the true sacrum. Some comparative anatomists call that cervical vertebra the 'first dorsal' in which the pleurapophyses retain, or begin to regain, their moveable articulations: but this character varies in different individuals of the same species. I have even found the pleurapophysis of the last cervical vertebra anchylosed on one side and not on the other.

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* Cuvier, Leçons d'Anatomie Comparée, i. (Ed. 1799, p. 170; Ed. 1836, p. 206).

The retention by the pleurapophyses of moveable articulations with the centrum, might also seem a good character of dorsal vertebræ at the hinder end of the series; but it is inconstant: I have found those elements anchylosed in one individual and free in another of the same species, in the anterior vertebræ, which are sacral by coalescence. All those vertebræ may be called for convenience 'sacral' in the bird, which are confluent by both centrums and neural arches with each other and with the iliac bones; and this confluence is so complete that it usually requires a vertical section and reference to the nerve-outlets in order to determine their number. The free vertebræ that succeed these are the caudal, of which the last, as in most osseous fishes, is a coalesced congeries of several, though for convenience, counted as one, and called in ornithotomy the plough-share bone (*c*, *s*, *h*). Although so many segments of the bird's skeleton are modified to transfer the weight of the horizontal trunk upon the ilia (62), the 'pelvis,' as in the crocodile, has but two hæmapophyses, 63, 64, below: it is characteristic of birds, however, that these are not united at their distal ends to their fellows of the opposite side, either with or without the intervention of a hæmal spine. The exception which the ostrich offers in regard to the anterior pair (pubic bone, 64) and that which the rhea presents in respect to the posterior pair (ischia, 63), serve to prove the rule of the inferiorly open pelvis in birds.

In regard to the diverging appendages of the two hæmal arches (scapular and pelvic) which have been selected for development into locomotive organs in all classes of vertebrata, the corresponding segments (carpal, 56, and tarsal, 66) agree in the paucity of their divisions, two bones in each, in all birds; and the succeeding segments (metacarpal and metatarsal) in consisting of three coalesced bones in both wing and leg, supporting digits answering to those marked II, III and IV, *ii*, *iii*, *iv*, in the crocodile. Such at least is their general character, the minor differences being the following:—In the hand-segment of the wing the anchylosed metacarpal of digit II is very short, represented as it seems only by its proximal end; those of the digits numbered III and IV attain their normal length, and are anchylosed together at the extremities only, with an interspace between their shafts.

In the metatarsus the three homotypal bones coalesce throughout their length, except in the penguin, where interspaces are left between their shafts or middle parts. But they also coalesce proximally with the two primitively distinct tarsal bones (66), whilst the metacarpals coalesce proximally with only part of the carpal series, if at all. And to the metatarsus there is usually superadded a rudimental, but unanchylosed, metatarsal bone of the digit answering to no I in the crocodile; but directed backwards, except in the swift. The numbers of the phalanges of the toes, *i ii* and *iii* in birds, correspond with those of their homologues in the crocodile: the toe *iv* has an additional phalanx, and the regular progression of the increase from 2 to 5, with one or two exceptions, is constant in the class, and serves to determine the toes in those birds in which they are reduced to three or two: thus, in the ostrich (fig. 11), the shorter of the two toes is determined by its greater number of phalanges, *s*, to be the homologue of the fourth in tetradactyle birds; and it is interesting to observe that the toe *iii*, notwithstanding its much greater length, has the usual smaller number of phalanges. But whilst unity of design is thus manifested, the wisdom of the Designer is displayed by the greater strength which results from the minor degree of subdivision of the part which takes the largest share in the support and propulsion of the body. The toe *v* is never present in birds, there is not even the rudiment of its metatarsal bone. The toe *i* is equally absent. (See paragraph at p. 193, on the spurs of the *Gallinaceæ.*)

Fig. 4 is the diagram of the skeleton of a typical mammalian quadruped; *e. g.* the dog (genus *Canis*). The modifications of the hæmal arch of the anterior segment resume the characters of those in the crocodile; the hæmapophysis (21) being the chief seat of development, and for the same purpose of extending its attachments, and adding to the firmness and strength of the henceforth immoveable maxillary arch. The diverging appendage from the pleurapophysis (20) is a single bone on each side (24), and in most mammals becomes confluent with the part of the posterior segment (6) against which it abuts.

The neurapophyses (14) of the anterior segment have coalesced together, as in birds, but are complicated, and their nature further obscured by anchylosis with ossified portions of the olfactory capsules, often extremely complex and extensive in the class Mammalia, in which the organ of smell attains its maximum of development. The neural spine (15), sometimes single, more frequently bifid, enjoys, agreeably with its extreme position in the series, a vast range of variety in its forms and proportions. In the rhinoceros it supports a dermal spine or 'horn.'

The second (frontal) segment presents unexpectedly a return to the archetypal character in a particular, in the absence of which all the lower classes of vertebrata depart from it, viz. the primitive independence of its centrum (9) from that (5) of the succeeding segment. The spine (11) of this, as well as those (7, 3) of the two following segments, continue, as in birds, to be the chief seat of the expansion requisite for the protection of the progressively developing brain. But in most mammals an additional element in the cranial walls is gained by the expansion of the distal end of the diverging appendage from the hæmapophysis (21) of the anterior segment. This appendage consists, as in birds and reptiles, of two pieces, and it is the second or most remote piece (27) which is the seat of the principal varieties, and especially of that squamous development which enables it not only to extend the points of fixation of the maxillary arch, but at the same time, to subserve the requirements of cranial space consequent on the large size of the cerebrum. The dismemberment called 'interparietale,' *x*, of the spine 3, has a less constant relation to the increased capacity of the cranium.

The pleurapophysis (28) of the second segment becomes, in the present class, still further displaced from its typical connections, and is even superseded in its typical functions by the intervention and development of 27. It is consequently much reduced in size, and strangely distorted in form in subserviency to the almost sole office that now remains to it, viz. the support of the tympanic membrane.

The frontal hæmapophyses and spine (29–32) have coalesced into a single bony arch, articulated by its extremities to the under part of the appendage 27.

The pleurapophysis (38) of the hyoid or third hæmal arch resumes in many mammals its typical connections with the parapophysis (*8*) of its proper segment; but its development is usually more or less restricted.

The articulation of the fourth (occipital) segment with the succeeding one called 'atlas,' is chiefly by means of zygapophyses (condyles) developed from the neurapophyses (*2*); the parapophyses (*4*) are likewise exogenous processes of the same elements.

The hæmal arch of the occiput (*51*, *52*), though in close proximity with its proper neural arch in some mammals, and in all mammals at the earlier period of development, is not directly articulated thereto, and sometimes recedes far from the rest of the skull.

The hæmapophysis (*52*) of the arch is ossified throughout its entire extent and the hæmal spine *52'*, below, in only one small exceptional order of the class (*Monotremata*). It becomes anchylosed with the pleurapophysis in all, and appears in the majority therefore as a mere process of *51*.

The single pair of cervical hæmapophyses (*58*) are more variable, both as to their extent of ossification and even existence.

The body of the atlas continues subject to the same modification of development from two centres with coalescence of one portion with the next centrum, which characterises it in all the other vertebrates above Batrachians*.

The confluence of the centrum with the neural arch takes place in every vertebra of the trunk; and the pleurapophyses, which are very short in the seven segments that succeed the skull, here also commonly coalesce with the other elements, circumscribing the lateral foramina for the 'vertebral' arteries. With the exception of the detached bones *58*, they are the only ossified parts of the hæmal arches of those segments.

The constancy of the number, *seven*, of the segments so modified, is truly remarkable and characteristic of the class Mammalia. It is true that the number is established at a very early stage of development, when the neck is alike short in all; and its law must be sought for in the circumstances, such as the existence of a complete diaphragm in the mammalia, which determined the number and distribution of the pairs of cervical nerves, upon which the development of the cervical vertebræ more immediately depends. The exceptions to the number *seven*, viz. *six* in the manatee, and *eight* or *nine* in the three-toed sloths, serve to establish the rule.

The eighth segment of the trunk in mammalia, like the tenth in the crocodile, has a complete hæmal arch, and here therefore the 'dorsal' series begins; but the hæmapophysial elements are rarely ossified in the present warm-blooded class.

The pleurapophyses (*pl*) of these arches are not only moveable, but are subject to a slight displacement, and their articulations, like those of the neurapophyses in the bird's sacrum, extend over the interspace of their own and a contiguous centrum.

The hæmal spines (*60*, *61*, *hs*) commonly remain distinct, and form a chain of ossicles corresponding in number with the complete hæmal arches, but they coalesce with each other in some of the higher mammalia, and are called collectively 'sternum.' (See p. 158.)

As the segments recede the pleurapophyses become shorter, return to their proper vertebra, and usually become appended to its diapophyses; the hæmapophyses also become shorter, and terminate at first by abutting against their antecedents, and finally by projecting freely.

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* See p. 93, and Annals of Natural History, vol. xx. p. 217.

These segments are followed by others (L) in which only the pleurapophysial parts (*pl*) of the hæmal arch are ossified, and these parts coalesce with the diapophyses (*d*).

Then come the segments (S) which, like those of the skull, are the seat of the modification by anchylosis, and of great and peculiar development of two of the hæmal arches in connection with them; the nature of the deviations from the typical standard which characterise the province of the endoskeleton called 'sacrum' and 'pelvis,' has been explained at pp. 158–161. In most mammals a greater number of segments is involved in this metamorphosis than in reptiles, in none are so many the seat of it as in birds. In the cetacea the modification by anchylosis is transferred to segments at the fore-part of the trunk, their 'sacrum' may be said to be in the neck; none of the post-abdominal vertebræ are subject to it any more than in serpents, fishes, or the extinct marine reptiles (*Enaliosauria*).

Great diversity of form, number and degree of development prevails in the vertebræ that succeed the sacrum in mammalia. Short pleurapophyses are developed at the extremities of the diapophyses of the anterior ones and coalesce with them. The hæmapophyses, when present or ossified, are articulated, as in reptiles, to the centrum directly, and alone form the hæmal arch. The terminal vertebræ are reduced to the central element, and rarely anchylose together.

The anterior anchylosed and expanded vertebræ are the cranial, Cr.

Those usually free vertebræ with short pleurapophyses, anchylosed to both their centrum and neural arch, are called 'cervical,' C. In some whales and armadilloes all or some of these vertebræ coalesce into one mass.

The series with moveable and usually longer pleurapophyses is called 'dorsal,' D.

Those with pleurapophyses confluent or connate with the extremities of the diapophyses are called 'lumbar,' L.

The succeeding vertebræ which anchylose together are called 'sacral,' S.

The rest are 'caudal,' Cd.

The modifications of the diverging appendages of the scapular and pelvic arches are numerous in kind and extreme in degree: with the exception of the cetacea, in which the hinder pair is absent—the cheiroptera, in which the fore-pair is specially developed for the actions of flight—and some burrowers, as the mole—a close analogy is commonly kept up between the two pairs: both, for example, are reduced to the same degree of simplicity in the solidungulous horse; both arrive at almost the highest stage of development, in the special adaptation of one of the digits to react upon the rest as an opposable thumb in both the fore- and hind-feet of the quadrumana.

Fig. 15, bones of the fore-limb, and fig. 16, bones of the hind-limb, of the wombat, illustrate the serial homology* of those bones, explained at pp. 166–168.

* It is with pleasure that I see any of the new terms proposed in my "Lectures on the Vertebrata" (1846) and "Report on the Archetype and Homologies of the Vertebrate Skeleton" (Report of the sixteenth meeting of 'the British Association held at Southampton in 1846'), and in earlier publications, as the "Geological Transactions for 1838," sanctioned by an original author like that of the 'Comparative Osteology,' folio, 1847, before cited. Thus Mr. Maclise says, "The laws of symmetry or Serial Homology preside over the genesis of formation."—Remarks on plate 49. And again:—"But in each of these three series of distinct parts, in that of spinous processes, of *neural arches*, and of bodies of vertebræ." "The spinous process, the *neural arch* and the vertebral body are structural varieties."—Explanation of plate 3. Whether the adoption of such terms as 'neural arch,' 'serial homology,' &c. be implied or acknowledged, the gratification is the same, provided they are not turned from their original sense. By 'neural arch' I mean both 'neurapophyses' and

53, 'humerus,' is the homotype of *65*, 'femur.'
54, 'ulna,' is the homotype of *67*, 'fibula.'
o, 'its olecranon,' is the homotype of *67'*, 'fabella,' or the sesamoid bone articulated to the produced and expanded head of the fibula.
55, 'radius,' is the homotype of *66*, 'tibia'*.
sc, scaphoid portion of 'os scapholunare,' is the homotype of *sc*, 'scaphoides.'
l, lunar portion of 'os scapholunare,' do. of *a*, 'astragalus.'
cu, cuneiform portion of 'os scapholunare,' do. of *cl*, articular part of 'calcaneum.'
p, 'pisiforme' is the homotype of *cl'*, fulcral part of 'calcaneum.'
t, 'trapezium' do. of *ci*, inner cuneiform.
z, 'trapezoides' do. of *cm*, middle cuneiform.
m, 'magnum' do. of *ce*, outer cuneiform.
u, 'unciforme' do. of *b*, cuboides; both of these representing two distinct carpals coalesced, as the scapholunar in the carpus represents the astragalus and scaphoid in the tarsus, and the calcaneum reciprocally the cuneiform and pisiform bones.

The serial homologies of the carpals and tarsals are better illustrated in the hand (Pl. II. fig. 13) and foot (fig. 14) of the orang, as will be presently explained.

With regard to the digits, they never exceed five in number in mammalia, and with the exception of the cetacea, the number of phalanges is limited to two in the first, I and *i*, and to three in each of the other digits, in both fore- and hind-feet. The first or innermost digit, as a general rule, is the first to disappear; in the hind-foot of the orang (fig. 14) commonly, and in that of the wombat, fig. 16, constantly, its short metatarsal supports but one phalanx; in the dog, taken as the type of the class (fig. 4), the inner digit is usually wanting in the hind-foot, and is always very diminutive in the fore-foot. The first digit of the hand is reduced to a short metacarpal in the spider-monkeys (*Ateles*).

The outer digit V and *v* is the next to disappear. In the tapir it is wanting in the hind-foot; and in the rhinoceros (fig. 17) in both hind- and fore-feet.

In the bisulcate quadrupeds the development of the second digit (II and *ii*) is arrested in addition to the two extreme ones (I and V), and the functions of support and progression are committed to the equally and symmetrically developed 3rd and 4th digits *iii* and *iv*. In most of the ruminants rudiments of the 2nd and 5th digits are retained (as at *ii* and *v*, fig. 18); but in the camel-tribe they have entirely disappeared together with the first digit, I and *i*.

'neural spine,' or the totality of the distinct parts of which such arch is composed. And I am of opinion that the parts of the neural arch which I have called 'neural spine' (spinous process), neurapophysis ('neural arch,' Maclise), together with the basis on which the arch rests, called 'centrum' or 'vertebral body,' are not 'structural varieties,' but the most constant and important elements of the typical segment or vertebra. I have been also led to conclude, with other physiologists, that other laws besides those of 'serial homology' preside over the formation of the animal body. The text of the body of my present work was struck off, with an alteration of the paging and a few corrections immediately after the printing of the "Volume of the Reports" in which it originally appeared, and several months before I received the valuable presentation copy of the work with which Mr. Maclise has favoured me. This must be my excuse to him for not noticing his work in an earlier part of the present one.

* The tendon of the triceps femoris is not ossified in this species, where it passes over the knee-joint at 66'; it resembles in this respect its homotype, the tendon of the biceps brachii, in the fore-limb.

In the horse (fig. 19) the fourth digit is the additional subject of arrested development, and the median one in both fore- and hind-feet, III and *iii*, is the last and sole digit which retains its full and functional development, thus manifesting its character as the most constant and essential of the terminal ramifications of the primitive ray. Rudiments of the metacarpals and metatarsals of the second and fourth digits (*ii* and *iv*, fig. 19) are retained, concealed beneath the skin; these 'splint-bones' of the veterinarian are duly adjusted to serve important uses, and their anchylosis and other abnormal conditions are a common cause of lameness; but the appreciation of their final purpose does not prevent the philosophic anatomist from recognising their real nature and archetypal relations, and thereby the essentially tridactyle character and true affinities of the genus *Equus*.

The carpal and tarsal ossicles undergo corresponding modifications, by confluence or arrested development, concomitant with this progressive simplification of the mammalian hand and foot. And here I am induced to offer a few observations on these bones in addition to the remarks contained in the text (pp. 167, 168).

Much difficulty has been experienced in determining the special homology of the carpal and tarsal bones in the lower vertebrates, more particularly the *Reptilia*, according to the names arbitrarily, in the first instance, applied to them, as they exist in the human skeleton. To gain a clear insight into their nature and relations, it becomes necessary to reverse the usual order of comparison, and to proceed from the lower vertebrates upwards. We first recognise a carpal segment of the fore limb in fishes, where it is represented by a series of short ossicles (fig. 2, *56*) intervening between the antibrachial bones (*54* and *55*) and the elongated rays or fingers (*57*) of the fin, and usually corresponding in number with the proximal or metacarpal series of those longer rays. When, in the air-breathing vertebrates, the typical number *five* is established, and governs, as a general rule, that of the terminal series of rays or digits, the number of ossicles or short rays at the base of these ought, theoretically, to accord in number with them; and when there are two series of such ossicles, there should be five in each. As regards the second or distal row, this number is actually maintained as a general rule in the order *Chelonia*. The metacarpal bones of the two outer digits are commonly each supported by a disiinct carpal ossicle (fig. 12, *u* and *u′*), and these two carpal bones obviously answer to that single one in *Mammalia* (*u*) which supports the metacarpal bones of the fourth and fifth, or two outer digits (IV and V). In large and old turtles (*Chelone*) the same confluence sometimes takes place which converts the two outer bones of the second carpal series into the 'os unciforme' of anthropotomy; and I have seen an instance in *Chelone Mydas* in which the 'os magnum' had also partially coalesced with the 'unciforme.' With regard to the homology of the distal carpal bones, supporting respectively the pollex and index, there can be no difficulty; one is the 'trapezium' (fig. 12, *t*), the other the 'trapezoides' (*ib.* *z*), and the bone supporting the middle digit, III, is obviously the 'os magnum.' The determinations of the bones of the proximal row is at first sight less easy; we have said that they are theoretically five in number, and we find so many actually in most *Quadrumana*, even in the anthropoid orang*. In this species two of the series (fig. 13, *s*, *s′*) answer to one in the human carpus, namely, the bone called 'scaphoides' (fig. 6, *sc*); that name is accordingly applied to the two inner or radial ossicles of the proximal carpal series in the orang, and they are considered as subdivisions of the 'os scaphoides'*. The 'lunare' (fig. 12, *l*) is situated on a plane above or proximal of these, and is wedged into the distal interspace between the radius and ulna. The pisiforme (*ib. p*) descends, or is placed more distal, and articulates with both the 'cuneiforme' (*ib. c*) and the outer 'unciforme' (*ib. u*).

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* Zool. Trans. i. 1835, p. 365.

In many *Chelonia*, as in *Testudo Elephantopus*, *Testudo græca*, in large individuals of *Chelone mydas*, the two inner or radial ossicles of the proximal carpal series are distinct as in the orang; they obviously, therefore, represent the human 'scaphoid,' and the scaphoid only. Ossification commences in that portion which is nearest the middle of the wrist, or which relates to the 'trapezoides' and index digit in younger *Chelones*: in some *Emydes*, as *Chelodina longicollis*, this is the only portion of the scaphoid which is ossified; in other species again, as *Testudo indica* (at least in old individuals), in *Cistudo clausa* and in *Emys europæa* (fig. 12, *s*), these two portions coalesce, and so form a single scaphoid bone, as in man.

In all *Chelonia* the next bone of the proximal row of the carpus (fig. 12, *l*) holds a higher or more proximal position than the rest, and is more or less wedged into the distal interspace between the radius and ulna; this, therefore, is plainly the homologue of the 'lunare' in the orang (fig. 13, *l*); it is theoretically, and in most *Chelonia* actually, the third bone of the proximal row of the carpus. The next bone towards the outer side which articulates exclusively with the ulna is the 'cuneiforme' (*ib. c*): usually it terminates the proximal series, but sometimes, as in *Cistudo clausa* and *Emys europæa* (fig. 12, *p*), it supports a small 'pisiforme;' and this bone, which is more developed, elongated and compressed in the turtles, articulates, as in the orang, in greater proportion with the 'unciforme' than with the 'cuneiforme.'

In the proximal row of the tarsus in Chelonia, one never finds more than two bones; and sometimes, as in the old *Testudo græca*, these have coalesced into one. The larger of the two, in most *Chelonia* (when they are distinct), articulates proximally with both tibia and fibula, crossing their interspace, and distally with all the bones of the second row except the outermost. It therefore answers to both the 'astragalus' and the 'naviculare' in the human tarsus, and sometimes also, as in the *Testudo græca* above cited, to the 'calcaneum.' The distal series of tarsal bones, like their homotypes in the carpus, are five in number in all Chelonia; the innermost, which supports the metacarpus of the hallux, answers to the 'os cuneiforme internum;' the second to 'o. c. medium;' the third to the 'o. c. externum;' the fourth, which supports the fourth metatarsal, answers to the inner or tibial half of the 'os cuboides;' the fifth, which sustains the fifth digit, to the outer half of the 'os cuboides.'

Thus, in the human carpus, the scaphoid (fig. 6, *sc*) and the unciforme (*u*) are each two connate carpal bones, and they actually manifest this theoretical division in most *Chelonia*. In the human tarsus the os naviculare (*ss*, *s*), the calcaneum (*cl*, *cl'*), and the cuboides (*b*), are each theoretically a compound of two bones; but in the Chelonia the principle of coalescence extends further: there are but two bones in the proximal row; three bones being represented by the larger, and two by the smaller of the proximal tarsals; on the other hand, the five bones of the distal series maintain their normal or typical distinctness.

In the crocodile a single bone of the carpus (fig. 3, *sli*) represents the two divisions of the scaphoid, as well as the lunare, the trapezium and trapezoides; a second bone (*c*) answers to the 'cuneiforme,' and there is a small

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* Vrolik, Anatomie Comparée du Chimpansé, fol. 1841.

'pisiforme (*p*);' the bone *u* represents a small 'magnum' and 'unciforme.' In the tarsus, ossification extends from the astragalo-navicular bone *asc*, and takes the place also of the internal and middle cuneiform bones. There is an external cuneiform bone, and a single bone *b* supports the two outer toes, and represents both divisions of the 'cuboides' in the Chelonia. In some Saurians the calcaneum retains its true or theoretical character, the articular portion (fig. 3, *cl*) being distinct from the fulcral or sesamoid portion (*cl'*).

In the dog and other carnivora, and in the wombat, the scaphoid is connate with the lunare; three carpal bones in the wrist of the orang are here therefore represented by one. In the hind-foot of the rhinoceros (fig. 17) the internal cuneiforme is gone, together with the digit it would have supported. In the ruminant the cuboid has coalesced with the navicular (fig. 18, *b s*). In the horse the external cuneiform (fig. 19, *ce*) is the largest of the distal row corresponding with the enormous toe which it supports; and the navicular, *s*, remains distinct from the cuneiform, *b*, which we may suppose to be represented by that portion which in the Emys supports the fourth toe.

In the ruminant the fibula is reduced to a small ossicle (fig. 18, *cr*), representing its distal end, wedged between the tibia and the calcaneum: the ulna is almost as much reduced in the fore-limb, and is commonly anchylosed to the radius. The two metacarpals of the principal digits, III and IV, coalesce to form the single cannon-bone, and the two corresponding metatarsals are subject to a like coalescence (fig. 18), a single bone supporting the fully developed toes, as in the bird: the rudimental back-toes, *ii* and *v*, have small detached metatarsals when they exist. Whilst the number of toes is thus seen to fall short, progressively, of five, the typical character of that number is still indicated by the power of determining the particular toe or toes of the five in man, which are retained in the tetradactyle, tridactyle, didactyle and monodactyle feet respectively of the lower mammals. But although the number 'five' thus governs the development of digits, properly so called, in all existing air-breathing vertebrata, the tendency to multiplication of terminal rays in the diverging appendages developed for locomotion may be seen to manifest itself in the sexual 'spurs' of the *Gallinaceæ* and *Monotremes*; in the hereditary supernumerary toes in certain varieties of the common fowl, and even in some individuals of the human race. But the single spur of the tetradactyle cock is not more a homologue of a normal digit in a pentadactyle reptile or mammal, than is the spur of the *Platypus*, or the second spur in the *Pavo bicalcaratus*.

Having thus noticed some of the chief varieties of the mammalian modification of the vertebrate archetype, there remains to add only a few words in explanation of fig. 6,—the diagram of the human skeleton.

As this is that which the anatomist has been accustomed to hear described most frequently and exclusively by the special terms, and according to the special views and ends of anthropotomy, the language in which its deviations from the common archetype have now to be noticed will probably appear strange and bizarre. The comprehension of the explanation will be facilitated by reference to the special name of the bone through its numeral in the column of names whenever such bone is alluded to under its general or archetypal name.

In the first and, notwithstanding the upright posture, the most anterior of the cranial segments, by reason of their forward curvature, the hæmapophysis (21) coalesces early with its own moiety of the divided spine ([illegible]), and the same thing happens to the next hæmal arch (20) with subsequent obliteration of the symphysis between the halves of its spine ([illegible]).

The pleurapophysis (20) of the first arch remains a distinct bone: its diverging appendage (24) coalesces with and becomes a 'process' of the centrum (5) of the parietal vertebra.

The neurapophyses (14) of the anterior segment are modified as in other mammalia, *i. e.* become confluent together and with the olfactory capsules; but appear externally below the orbital process of the frontal.

The spine (15) is small, but bifid.

That of the second segment (11) attains its maximum of development, as do also the spines of the two following vertebræ (7 and 3). The bifid spine of the parietal segment is truly enormous as compared with that of the fish (fig. 2, 7) or the reptile (fig. 3, 7), in which latter animal the spine, being undivided, adheres closer to the archetype.

The diverging appendage (26, 27) from the hæmapophysis (21) is divided into two pieces, as in most mammals and reptiles; both are broad and flat: the first (26) serves to fix the arch to the parapophysis (12) of the second segment, from which it is here dislocated; the portion (27), which becomes enormously expanded, covers a large vacuity between the third and fourth neural arches, and overlaps by a squamous suture part of the expanded spines of both those vertebræ. It also anchyloses below with the pleurapophysis (28) of the second segment, with the parapophysis (8) and the pleurapophysis (38) of the third segment, as well as with the bony capsule of the organ of hearing (16), forming with those parts the most singularly complex 'cranial bone' of anthropotomy.

The centrums (5, 9) and neurapophyses (6, 10) of the second and third segments coalesce with each other, and with the first pair of diverging appendages (24) of the anterior hæmal arch (20, 21, 22), forming the complex 'sphenoid' bone of anthropotomy.

The centrum (1), neurapophyses (2), and neural spine (3) of the fourth segment speedily anchylose together, and their centrum afterwards coalesces with that (5) of the parietal vertebra, forming the still more complex cranial bone called 'os spheno-occipitale' by Soemmering.

The hæmapophyses of the third much-reduced hæmal arch (40) are ossified only at the extremity which joins the spine (41): the remainder of the hæmapophysis is continued in a ligamentous state to their anchylosed pleurapophyses (38), forming the 'styloid processes of the temporal bone.'

The detached and displaced pleurapophyses (51) of the occipital vertebra attain considerable breadth: their hæmapophyses (52) are ossified only at the extremity which joins the pleurapophysis, and with which it coalesces. The diverging appendage (53–57) here attains its maximum of adaptive development; as in the skate-fish (*Raia*) it exhibits the extreme of vegetative or polaric growth. But the progressive steps by which it departs from the primitive or archetypal simplicity, shown in figures 7 and 8, are so gradual that the special homology of the arm and hand of man with the bifid-jointed appendage of the scapular arch in the amphiuma, and with the simple jointed ray of that of the scapular arch of the lepidosiren, has never been doubted or called in question. In ascending, therefore, to the higher generalization of the signification, or relation to the archetype, of such simple, or bifid, jointed or more complicated appendage of such scapular arch, we are compelled by the truth, as it exists in nature, to admit that the scapular arch in the lepidosiren and other fishes forms the inferior costal or hæmal arch of the occipital segment or vertebra; and, by reference to the archetype, to see in the diverging appendage of such arch, a repetition of similarly simple diverging appendages of succeeding segments. These, indeed, retain their primitive simplicity, as shown in the trunk-vertebræ of the fish (fig. 2, *a a*) and of the bird (fig. 4, *a a*); and that simplicity is very gradually departed from in the case of the appendages of the occipital vertebra, by the stages recognisable in figs. 7 and 8. If, then, it be admitted that the upper limb (arm and hand) of man is the homologue of the fore limb of the amphiume, of the pectoral fin of the fish and of the pectoral ray of the lepidosiren; it follows, that, like the latter, it must also be the 'diverging appendage' of the arch called 'scapular,' which is the hæmal arch of the occipital vertebra; and, therefore, however strange or paradoxical the proposition may sound, that the scapular arch and its appendages, down to the last phalanx of the little finger, are truly and essentially bones of the skull.

The centrum of the first segment of the neck is subject to the same modification as in the ordinary mammalia, the major part (*c a*) remaining anchylosed to the centrum of the succeeding segment (*c d*), of which it forms the 'odontoid process' in human anatomy. The cortical part (*c a*, *x*) is that which is usually called the 'body' of the atlas: it is connected by aponeurosis to the corresponding part of the centrum of the occipital vertebra: the articulation of the head with the neck is chiefly by means of zygapophyses developed in the form of convex condyles from the neurapophyses (*s*); and received by the concave zygapophyses of the neural arch of the atlas. In the other cervical segments, the autogenous elements of which they are composed are represented diagrammatically in fig. 6 as distinct, viz. the centrum, neurapophysis, neural spine, and pleurapophysis; the latter element in the seventh vertebra sometimes attains a length nearly equal to that of the first dorsal. In the eleventh dorsal vertebra the elements are additionally indicated by the initial letters. The cervical hæmapophyses (*ss*) are wholly ossified and well-developed. The hæmal arches in the abdominal region retain their aponeurotic texture: the anchylosed and stunted pleurapophyses are continued by the tendinous origins of the 'transversus abdominis;'* the hæmapophyses are the 'inscriptiones tendineæ recti abdominis;' and the basis of the hæmal spines is the 'linea alba.' But these and other modifications of the bones of the trunk have been described at pp. 158–161.

On reviewing the figures in Plate II. it will be seen that the disposition of the whole vertebral column has changed with the progressive modifications of its segments: it soon departs from the geometric simplicity of the archetype, and exchanges the straight line for the curve or a succession of curves.

In the fish the deviation is least: the whole column is straight in some; or it describes but one slight curve, convex dorsal, from the nasal to the caudal vertebræ: some fishes show a slight upward curve of the latter.

In the lower reptiles the whole spine is straight, or simply curved as in fishes: in crocodiles the general curve, extending from the segments of the head along the back of the tail, is interrupted by a slight bend of the neck in the opposite direction.

In the bird, the longer and more slender neck is the seat of an elegant double or sigmoid curve; the segments of the head are directed at right angles to the chord of the cervical curves; and the tail bends upwards in a direction contrary to that of the fixed part of the trunk.

The degree and variety of the curves of the vertebral column vary much in mammalia, according to the medium and mode of their locomotion. In the subject of the diagram (fig. *s*), the cranial segments form a slight angle with the cervical ones; and these form another with the dorsal segments; the curve of the back is slightly reversed in the loins, and again resumed in the sacrum and base of the tail; which latter is the seat of extensive and variable degrees of flexuosity, its extremity being spiral and prehensile in some quadrupeds. Another mark of adaptive modification may now be seen in the convergence of the spines of the cervical vertebræ towards that of the fourth of this series, and by a more marked convergence of the spines of the dorsal and lumbar vertebræ towards that of the eleventh of the dorsal series: both these points of convergence indicate centres of special motion in these regions of the spine. That in the back commonly relates to the bounding mode of progression of the animal, in which the spine is alternately bent and extended, upon the vertebra with the vertical spine. When the quadruped moves along with a rigid spine by rapid walking or a kind of stiff trot, as in the heavy pachyderms, the spinous processes of the dorsal, lumbar and sacral vertebræ all bend in one direction—slightly backwards—and no centre of motion is indicated by a point of convergence. The elephant and rhinoceros resemble in this respect the stiff-backed crocodile.

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* See Albinus, 'Historia Musculorum,' Tab. XIV. fig. 3.

In the human frame the succession of slight but graceful curves, and their relation to diffusing shocks and balancing the body in the erect position, have been explained in various estimable physiological works.

In no species do the cranial vertebræ bend at so strong an angle from the chord of the opposite curve of the neck: and in none is the curve of the sacrum and coccyx so strong in proportion to the small number of the vertebræ.

But the most striking characteristic of the human modification of the endoskeleton is the enormous development, both in bulk and special adaptive modification, of the two pairs of diverging appendages retained for the purposes of support, locomotion and prehension. In no mammal does the length of the pelvic appendages, as compared with that of the vertebral column, equal that in man.

Perhaps the greatest obstacle to the contemplation of these members as homologues of the simple diverging rays (*a*, *a*) of the hæmal arch of the typical vertebra, as they are shown in the archetype, and in many segments of the bird and fish, will arise from the early and habitual contemplation of them by the anatomist under their maximum condition of growth and development in its completest sense in man.

In the skate (*Raia*) the pectoral members surpass in relative bulk their homologues in man: but the development of these appendages is of a lower kind: it consists of a vegetative repetition,—division, bifurcation and segmentation—of mere rays, of a multiplication of essentially similar parts, without power of reciprocal action and reaction on one another; all being bound up in one common fold of integument for one simple action—the only one required for an animal so low in the scale, but perfectly provided for by the form of fin in question. At first sight the pectoral fin of the skate with its hundred digits seems a more complex deviation from the primordial single ray, as shown in the lepidosiren (fig. 7), than the pentadactyle upper extremity (53–57) of man; but the complexity is more apparent than real. The high characteristics of the human arm and hand are manifested by the subordination of each part to a harmonious combination of function with another, by the departure of every element of the appendage from the form of the simple ray, and each by a special modification of its own; so that every single bone is distinguishable from another: each digit has its own peculiar character and name, and the 'thumb,' which is the least constant and important of the five divisions of the appendage in the rest of the class, becomes in man the most important element of the terminal segment, and that which makes it a 'hand' properly so called.

In the pelvic, as in the scapular extremity, the same digit (*i*), which is the first to be rejected in the mammalian series, becomes, as it were, 'the chief stone of the corner,' and is termed 'par excellence,' the 'great toe:' and this is more peculiarly characteristic of the genus *Homo* than even its homotype the thumb; for the monkey has a kind of *pollex* on the hand, but no mammal presents that development of the *hallux*, on which the erect posture and gait of man mainly depend.

We perceive, however, that although the first toe (fig. 6, *i*) is the longest as well as the largest, it retains its characteristic inferior number of phalanges; its bulk depending, like the larger toe in the didactyle ostrich, on the superior size instead of an increased number of bones; whilst the fifth or little toe (*v*) still retains with diminished proportions its full complement of phalanges. The teleologist will discern that the requisite strength of the toe, which is the chief fulcrum when the whole body is raised by the power acting on the heel, as in stepping forward, has been regarded in the diminished number of its joints; but the same final cause would not appear to have governed the different number of the equally-sized first and fifth of the five toes inclosed in the massive hoof of the elephant or the webbed hind-paddle of the seal: and whether the hallux be the shortest of the five or the longest, it has always the same number of phalanges whenever it is present, provided it supports a nail, a hoof or a claw, in the mammalian series.

The satisfaction felt by the rightly constituted mind must ever be great in recognising the fitness of parts for their appropriate functions; but when this fitness is gained, as in the great toe of the foot of man and the ostrich, by a structure which at the same time manifests a harmonious concord with a common type, the power of the One Great Cause of all organization is appreciated as fully, perhaps, as it is possible to be by our limited intelligence.

It is interesting to perceive both in the human hand and foot that the digits that have been most modified either by excess or defect of development are precisely those that are the least constant in the mammalian series, the two, for example, that form the extremes of the series; whilst the three intermediate digits are more conformably and equably developed. In the hand, the 'digitus medius'—the most constant of all in the vertebrate series, and most entitled to be viewed as the persistent representative of the terminal segments of the primitive elementary ray,—still shows a slight superiority of size; though few, perhaps, are aware that the bones forming the three joints of this finger answer to those called 'great pastern bone,' 'little pastern bone,' and 'coffin bone' in the horse, and that the nail of this finger represents the hoof in the horse.

In the human foot the three more constant toes, *ii*, *iii*, *iv*, maintain more equality of size than their homotypes in the hand: the middle toe here also is the representative of the chief part of the hind-foot of the horse: but the fourth toe answers to that which, by excess of growth, becomes the chief member of the long and strong hind-foot of the kangaroo. These and the like relations to the vertebrate archetype, which, together with the principle of the fitness of things, govern the forms and proportions of parts of the human frame, cannot but be both interesting and useful to the artist, as being calculated to call his attention to differential characters, which, though constant, may be so slight as to escape attention until their true significance is made known.

The few examples of unmutilated feet from the works of the ancient Greek sculptors show, indeed, how truly their just observation of nature supplied the insight into the archetypal law, and guided them to an exact and beautiful indication of the affinities of the three middle toes as contrasted with the first and fifth, the distinctive characters of the last being as truly given as those of the great toe.

In 'Il Giorno'—the chef-d'œuvre of CORREGGIO at Parma, in some respects the noblest production of modern painting—these characters have been overlooked in the foot of the kneeling Magdalen, in which the toes progressively decrease in equable proportion from the second to the fifth. The same fault may be seen in the right foot of the Mercury in the painting, No. 10, in our National Gallery, attributed to the same great artist, and with which the beautiful right foot of the dead Saviour in the adjoining painting by the more truthful and severe FRANCIA favourably contrasts. Both the Venus and Cupid in the GUIDO of the same Gallery afford examples of the conventional foot, whilst that (the left one) of the Christ in the 'Raising of Lazarus' by Sebastian del Piombo is an example of the beautiful and the true.

To return from this digression to the immediate subject (fig.6) of the present explanation, besides the 'bones' indicated by the figures and named in the adjoining column, the following are referred to by letters:—in the carpus (*ss*), *sc* is the 'scaphoides,' *l* the 'lunare,' *cu* the 'cuneiforme,' *p* the 'pisiforme,' *t* the 'trapezium,' *z* the 'trapezoides,' *m* the 'magnum,' *u* the 'unciforme;' in the tarsus (*ts*) *s* is the 'scaphoides' or 'naviculare,' *a* the 'astragalus,' *cl* the articular part of the 'calcaneum,' *cl'* 'its fulcral part,' *c i* is the 'cuneiforme internum,' *c m* the 'cuneiforme medium,' *c e* the 'cuneiforme externum.'

In the hand, the bones or segments of the rays immediately supported by the carpus are called 'metacarpals,' the corresponding series in the foot 'metatarsals:' the remaining segments are called 'phalanges;' those nearest the trunk are 'proximal;' those furthest from it and supporting the nail 'distal' or 'ungual;' the intermediate ones are the 'middle phalanges;' the middle phalanx is absent in the thumb and great toe. It is only in the horse that the phalanges, from their great and peculiar development and frequent disease, have received special names: the hippotomist, in this respect, having done exactly what the anthropotomist had done before in regard to other bones, and for the same good reason. Both, however, will appreciate the necessity of knowing something more of a bone, besides its specialities of form and structure in relation to its uses and diseases, in order fully and truly to understand it. Some knowledge of the archetype, indeed, would seem to be required to enable the anthropotomist to appreciate even the differences of conformation and proportion which must strike his eye in contemplating the immediate object of his descriptions. In the elaborate article on the 'Bones of the Foot,' for example, in the 'Cyclopædia of Anatomy and Physiology' by its accomplished editor, it is stated:—"The toes are numbered from the inner or great toe; they gradually diminish in length from the first to the fifth:"—"All the metatarsal phalanges possess these general characters: that of the great toe is very considerably thicker than the others, and is slightly longer: the remaining ones differ but little in size," vol. ii. p. 342. Now, besides the difference in degree of diminution observable in the skeleton of well-formed feet, and especially in the races where no artificial compression has been applied to the foot during growth, the proximal phalanx of the little toe is broader and more depressed in proportion to its length; those of the three middle toes being narrower or more compressed at the middle of their shafts*.

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* How little the true nature of the science of comparative anatomy, or anatomy rightly so called, is comprehended, and its indispensable aid to a true understanding of anthropotomy recognised, may be inferred by the definitions of the science of 'Anatomy' in the latest summaries of human knowledge published in this country. Thus in the excellent 'Penny Cyclopædia' we read that "Comparative anatomy includes an account of the structure of all classes of animals *excepting that of man*; Human anatomy is restricted to an account of the structure of man only," vol. i. p. 198. Art. Anatomy.

In fig. 5. the typical dentition of the placental mammal is shown, viz. that expressed by the formula:—$i\frac{3-3}{3-3}$; $c\frac{1-1}{1-1}$; $p\frac{4-4}{4-4}$; $m\frac{3-3}{3-3}=44$: which signifies that there are on each side of both jaws three incisors (*i*, 1, 2, 3), one canine (*c*), four premolars (*p*, 1, 2, 3, 4), and three molars (*m*, 1, 2, 3). The fourth premolar in the upper jaw and the first molar in the lower jaw are called 'sectorial' or 'carnassial' teeth in the carnivora. In the human subject the dentition is:—$i\frac{2-2}{2-2}$; $c\frac{1-1}{1-1}$; $p\frac{2-2}{2-2}$; $m\frac{3-3}{3-3}=32$; and the absent premolars are the first and second of the typical formula*.

Fig. 7. Hind view of the occipital vertebra of the *Lepidosiren* (*Protopterus*) *annectens* (from nature). The *letters* indicate the bones in their general relation as elements of the primary segment, the *numbers* their special names.

All the bones of the fore-limb, from the humerus 53 to the manus 57, are potentially included in the segmented ray *a*.

Fig. 8. Hind view of the occipital vertebra of the *Amphiuma didactylum* (from nature). The general and special names and homologies of the parts are similarly indicated. The articulation of the head to the trunk is already here (in batrachians) transferred, as afterwards again in mammals, from the centrum to the neurapophyses (*n* 2), and the parts of the neural arch have coalesced together. The hæmal arch is detached from the neural arch, and slightly displaced backwards; but the pleurapophysis (*pl*, 51) retains its simple rib-like form and position, slightly inclining outwards below from the vertical line. The hæmapophyses (*h*, 52) do not pass beyond the state of gristle, but are much expanded: they resemble in their histological condition their homotypes, called 'cartilages of the ribs,' in the thorax of man. If the study of the essential nature of the detached inverted arch so formed had been begun at this point and compared with that of the vertebrates lower in the scale, no doubt, I apprehend, would have been entertained as to the detachment of such hæmal arch in the amphiuma being a deviation from type, and its attachment to the rest of its segment in the osseous fishes as being a retention of the typical structure: this condition would have been in point of fact the rule, and the other the exception. In extending the comparison to the higher classes, the instances of the detachment and distance of the scapular arch from the occiput predominate, and its attachment to that neural arch of the skull, in fishes, becomes numerically the exception.

The question then arises, whether the number of instances, or the circumstances under which the instances occur, are to be our guides in judging of adherence to or departure from the archetype. Fishes are the lowest of the classes of vertebrata, and if it be true that to understand the fundamental type of the vertebrate skeleton its study must be commenced, not in the highest species,—not in that skeleton where irrelative repetition is least and adaptive modification most displayed, but in the lowest class, where the reverse conditions prevail,—then the position and connections of the scapular arch in fishes must be regarded as more conformable to the typical structure than the altered position which that arch presents in all the higher classes: and in this conclusion we are supported by observing that the position and relations of the scapular arch in fishes render the cranial segment, of which it there forms part, more conformable with the other segments of the skeleton; whilst in the crocodile, for example, as explained at pp. 117–119, the occipital segment is unconformable by reason of the absence of its hæmal arch, and can only be made conformable by the restoration of the scapular arch to

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* For the determination of the teeth in mammalia, see my 'Odontography,' pp. 514–522.

the place it holds in fishes. For, in fig. 3, with regard to the three segments that precede the occipital one, there are three hæmal arches—maxillary, mandibular and hyoidean; and with regard to the segments which succeed the occipital one as far as the sacrum inclusive, every one has its pleurapophyses if not its entire hæmal arch. The scapulæ, therefore, being what fig. 7 shows them to be, pleurapophyses, the occipital segment in the crocodile is the only one in which those elements are wanting, and the scapulæ are the only pleurapophyses by which the want can be supplied in order to restore the type as it is displayed in nature by the class of fishes.

With respect also to the diverging appendages, *a a*, of the occipito-hæmal arch of the amphiuma, if the anatomist had observed them with a previous knowledge only of the lower class of vertebrata, the bones 54, 55 and 57 would doubtless have been regarded and described only as bifid segments of the primitive simple ray. But the parts having been originally studied from a higher point in the animal series, where the homologues of those segments by virtue of their special developments in adaptation to special functions had obtained special names, those names are naturally and properly transferred to their simplified homologues in the appendage recognized as the anterior limb or extremity of the amphiume: the proximal single segment 53 as 'humerus,' the ossified divisions of the next segment as 54 'radius' and 55 'ulna,' the terminal bifurcation as the 'digits.' This extreme instance of the unity of the plan upon which the limbs of the vertebrate animals have been constructed is a perfectly true one.

Cuvier has most accurately assigned their special names to each of the parts of the fore-limb in the amphiume in his celebrated memoir*. All that I would ask of his most devoted disciple is to reciprocate; to grant the inference as to the signification of the parts arrived at by their study in the ascending route of inquiry, which the homologist is ready to give to the determinations of the special character of the parts which have been obtained by comparisons pursued descensively from man: in other words, to admit that the whole (53–57) in the amphiume (fig. 7) may be the homologue of the ray (53–57) in the lepidosiren (fig. 6); that this may answer to the ray (53–57 *a*) in the fourth segment of the archetype (fig. 1); and that such ray is repeated in the diverging appendages, *a a*, of the succeeding segments of the skeleton: whereby we are led to the recognition of the essential nature of the limbs as developed diverging appendages of the hæmal arches of vertebræ, and the fore-limbs as being such appendages of the occipital vertebra†.

In fig. 9 the elementary condition of the hind-limbs in the vertebrata is shown in nature in a back view of the pelvic vertebra of the *Protopterus* or lepidosiren. The letters signify the general and the figures the special homologies of the parts. The apical elements (63) of the hæmal arch are detached from the basal ones (62) and the rest of the segment, and carry with them the diverging appendages (65–68), as in all other fishes.

Fig. 10 is the corresponding arch and appendages of the *Proteus anguinus*.

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* Dans ces deux figures *a* est l'*omoplate*, *b* les plaques sternales cartilagineuses formées probablement des *os coracoïdiens*; *c* l'*humerus*, suivi du *cubitus* et du *radius* qui portent un *carpe* cartilagineux et deux os *metacarpiens* et *phalangiens* osseux. Mémoire lu à l'Académie des Sciences, le 13 Novembre 1826, p. 15.

† The want of connection of a peripheral piece, at its peripheral border, appears to be one condition of its greater extent of variety of form and proportion than in the more central pieces of a natural segment. There is nothing to restrain its luxuriant development from a simple spine to a plate, to a divided plate with intercalations, &c., or to a lengthened segmented ray bifurcating and shooting out into additional segments with indefinite modifications of these.

Here the hæmal arch retains its natural connections with the rest of its vertebra, and henceforth preserves them, with a few exceptions (Enaliosauria and Cetacea), in all the air-breathing classes, up to and including Man. In respect of the modification by displacement, the numerical examples of adhesion to or departure from type are reversed in the pelvic segment, as compared with the occipital one. Mammals, birds and reptiles show the rule, and fishes the exception, typically as well as numerically. There has been, therefore, no difficulty or discrepancy of opinion in regard to the homology of the detached hæmal arch and its appendages in fishes. Cuvier saw in 63, fig. 2, the representative of the 'os innominatum' or 'os du bassin;' and, notwithstanding the degree of displacement to which such rudiment of a pelvis, with its pelvic members, were subject in fishes, Linnæus had as little hesitation in recognizing in the ventral fins the homologues of hind-limbs wherever they were placed. When in their normal position, as at v, fig. 2, they characterized the 'abdominal' fishes; when advanced to beneath the pectoral fins, as at v', they characterized the 'thoracic' fishes; when still more advanced, as at v'', they characterized the 'jugular' fishes. The species in which the ventral fins were absent were 'apodal,' in the philosophic language of the immortal Swede.

Now all that is here required, in regard to the determination of the locomotive members, is, that no more value be given to the character of detachment and change of place in regard to the scapular arch and its appendages than Linnæus allowed in the case of the pelvic arch and its appendages.

The arms are shifted to and fro in the bodies of the air breathing vertebrates, the legs in those of the water-breathing vertebrates: the arch supporting the arms is fixed in its true place in fishes, and the arch supporting the legs retains its true place in the higher classes; only it is often necessary that it should be so developed as to be applied to many segments besides the one to which it properly belongs. In the proteus (fig. 10), however, the ilium (62) retains its simple primitive rib-like form, just as the scapula does in fig. 8; and it is connected, as we saw likewise in the menopome (p. 159, fig. 28), to its proper vertebra exclusively. The segments of the bifurcated ray in the proteus have been determined by descensive comparison from the higher classes to be, 65, the femur; 66, 67, tibia and fibula; 68, tarsus; 69, metatarsus and phalanges.

Fig. 11. Distal half of anchylosed metatarsus, with the two toes, of the ostrich (*Struthio camelus*), answering to the third and fourth in tetradactyle birds.

Fig. 12. Bones of the fore-foot of a freshwater tortoise (*Emys europæa*): *s* outer division of 'scaphoides,' *s'* inner division of 'scaphoides,' *l* 'lunare,' *c* 'cuneiforme,' *p* 'pisiforme,' *t* 'trapezium,' *z* 'trapezoides,' *m* 'os magnum,' *u*, *u* the two divisions of the 'unciforme:' in this reptile the number of carpal bones is ten, five in each row, corresponding with the number of the digits.

Fig. 13. Bones of the hand of the orang-utan (*Simia satyrus*). The letters indicate the same parts as in the preceding figure. The two unciform bones have coalesced into one, and the number of carpal bones is nine. In the human hand, by the coalescence of the two radial bones of the proximal row to form the 'scaphoid,' it is reduced to eight.

Figure 14. Bones of the hind-foot of the orang-utan: *s*, 'scaphoides,' answering to *s s'* in the carpus; *a* 'astragalus,' answering to *l* in the carpus; *c l* articular part of 'calcaneum,' answering to *c* in the carpus; *c l'* fulcral part of calcaneum, answering to *p* in the carpus; *c i* 'cuneiforme internum,' answering to *t* in the carpus; *c m* 'cuneiforme medium,' answering to *z* in

the carpus; *c e* 'cuneiforme externum,' answering to *m* in the carpus; *b* 'cuboides,' answering to *u* in the carpus, and like it consisting essentially of two connate bones: by a similar connation of two bones in *s*, and also in *cl*, the number of tarsal ossicles is reduced, as in man, to seven.

Fig. 15. Bones of the fore-limb of the wombat (*Phascolomys wombatus*). The letters indicate the same bones as in fig. 12, but the lunare having coalesced with the two connate bones forming the scaphoid, the number of carpals is seven.

Fig. 16. Bones of the hind-limb of the wombat, showing the resemblance to the ulna in its homotype, the fibula 65, by its proximal enlargement, and the superaddition of the sesamoid ossicle 65', which answers to the olecranon, and becomes anchylosed to the fibula in the monotremes. The olecranon itself is a detached sesamoid in some bats. The hallux is reduced to a small metatarsal (1) and one rudimental phalanx, *i*. The letters signify the same bones as in the tarsus of fig. 14. The foot can be rotated like the hand.

Fig. 17. Bones of the hind-foot of the rhinoceros. The tarsus is reduced by the continued connate condition of *s* and of *cl*, *cl'*, and by the absence of *c i* and of the outer division of *b*, to six bones. The inner toe *i* and the outer toe *v* have disappeared.

Fig. 18. Bones of the hind-foot of the ox. By the connation of *b* with *s*, forming a scapho-cuboid bone, the number of tarsal bones is further reduced to five, and of these the cuneiforme medium is a mere rudiment attached to the back part of *c e*. The functional toes are reduced to two by the rudimental condition of the second *ii* and fifth *v*: the first being wholly absent.

Fig. 19. Bones of the hind-foot of the horse. Here the number of the tarsal bones is the same as in the rhinoceros, but the toes *ii* and *iv* are reduced to mere rudiments of their metatarsal segments, forming the 'splint-bones' of veterinary surgeons. Only the third toe is retained for the functions of the foot, which it almost exclusively represents.

With regard to the order of the descriptions of the cranial vertebræ, pp. 106–139. and of the numbers of the bones in the several figures, it may be asked why I have not begun to enumerate the segments of the head from the most anterior one in the archetypal figure, and the elements of the cranial vertebræ from the centrum of such anterior segment (vomer, 13), and why I did not count all the elements of that segment before going to the next? This order seems so natural, that it may one day be proposed, and perhaps supersede the order of enumeration here adopted. By those, however, who may view the prenasal and other supplementary ossicles in certain fishes and mammals that are anterior to the nasal vertebra, as rudiments of still more anterior vertebræ analogous to those abortive ones at the opposite extreme of the body, the commencement with the vomer as no. 1, would appear equally artificial and arbitrary, as being then regarded the centrum of the 2nd vertebra, or perhaps the 3rd vertebra of the head. It is therefore in order to secure a constant element to commence with, in all vertebrates, that I have begun with the basioccipital. It will be seen by a glance at the typical skeletons in Plate II., that the vertebræ in the middle of the body retain most of their typical character, whilst those at the extremities are subject to most modification: the direction in which the segments are counted must in any case be arbitrary, and in enumerating those of the skull the advantage of commencing with the one that certainly and invariably begins the cranial series determined my choice in counting from the trunk forwards; when if rudiments of segments should be determined anterior to the nasal one, in any animal, they may be reckoned as representing a 5th or 6th cranial vertebra. The order of enumeration of the constituent elements or bones being likewise to a certain extent arbitrary, I have chosen that which appears to me to guide to the most natural course of description of the skull in different animals.

I would entreat the innovator, therefore, to be well assured that he has better grounds than these for changing the order of enumerating the cranial vertebræ and their elements, before he does away with the advantage of having a number as a fixed and determinate symbol of a bone; which advantage would be gained to Anatomy if its cultivators should agree upon a given order of enumeration.

THE END.

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